

THE ROLE OF TERRESTRIAL HABITAT IN THE  
POPULATION DYNAMICS AND CONSERVATION OF  
POND-BREEDING AMPHIBIANS

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by  
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The undersigned, appointed by the dean of the Graduate School, have examined the dissertation entitled

THE ROLE OF TERRESTRIAL HABITAT IN THE  
POPULATION DYNAMICS AND CONSERVATION OF  
POND-BREEDING AMPHIBIANS

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**Dr. Raymond Semlitsch, Dissertation Supervisor**

**ABSTRACT**

Habitat loss and degradation are implicated in the majority of amphibian population declines in the United States and throughout the world. With a complex life cycle requiring both aquatic and terrestrial habitat, pond-breeding amphibians are especially vulnerable to changes in habitat quantity and quality. Conservation of aquatic breeding habitat is clearly essential for these populations, however, changes in terrestrial habitat quality that affect juvenile or adult survival can result in declines and increased extinction rates even when aquatic breeding habitat is protected. Because amphibian research has historically focused on the aquatic larval stage, less is known about terrestrial life history stages and their role in amphibian population dynamics. Recent demographic models have suggested that amphibian population trends are most sensitive to changes in terrestrial stage vital rates, emphasizing the need to better understand factors affecting the terrestrial life history stages of pond-breeding amphibians.

In my dissertation research, I used both demographic modeling and experimental field research to evaluate the role of terrestrial habitat in the population dynamics and conservation of pond-breeding amphibians. I have focused on questions that ask how the

quantity and quality of terrestrial habitat available to amphibians affects demographic rates and how these changes can affect populations.

Striking a feasible balance between human land-use and habitat conservation is one of the greatest challenges in efforts to conserve biodiversity. However, the specific risks of varying amounts of habitat loss are often difficult to quantify, hindering conservation efforts. In my research, I began by using data available in the literature to develop stochastic, stage-structured demographic models for two pond-breeding amphibian species, the wood frog *Rana sylvatica* and the spotted salamander, *Ambystoma maculatum*. I used these models to determine the potential effects of a range of core terrestrial habitat areas on population size and time to extinction for both species. These models offer a means of quantifying the risks associated with habitat loss and degradation. Model simulation results emphasize that the maintenance of viable pond-breeding amphibian populations is dependent on a sufficient quantity and quality of terrestrial habitat, as well as connectivity among local populations. Model simulations also highlight important species-specific responses.

Using the model building process to focus my research goals, I next carried out field experiments designed to improve model accuracy. In the first of these experiments I manipulated terrestrial densities of wood frogs and American toads (*Bufo americanus*) and followed the growth, survival and reproductive rates of individuals over the course of a year. Results from this experiment suggest that terrestrial density can affect vital rates of juvenile amphibians and should be considered in models of amphibian population dynamics. I also carried out field experiments to determine the effects of specific forestry practices on the survival of juvenile wood frogs and American toads. The results

of these experiments indicate that forestry practices interact with existing landscape structure to determine microclimate and thereby influence amphibian survival. Returning to the model building process, I used the results of my field experiments to develop a demographic model designed to evaluate the potential effects of specific forestry practices on the probability of persistence and size of local wood frog populations. I also used the model to predict the population level effects of reductions in immigration rates and to test the potential effectiveness of different management options in mitigating the effects of forestry practices. Model simulations demonstrated that changes in juvenile survival resulting from forestry practices can have substantial population level effects, increasing extinction probabilities up to 100%. However, the magnitude of these effects depends greatly on both the type of forestry practice employed as well as the proportion of emerging metamorphs affected.

The results of my research indicate that the quantity and quality of terrestrial habitat available to pond-breeding amphibians can affect juvenile survival, growth and reproductive rates, and that these changes can have substantial population level consequences including increased extinction probabilities and decreased population sizes. Future research will incorporate these results into spatially explicit models of amphibian metapopulation dynamics.

# CHAPTER 1

## INTRODUCTION

A recent assessment of the conservation status of the world's 5,918 amphibian species concluded that one-third are threatened and nearly half are experiencing declines in population size (Stuart et al. 2004). Since these declines were first recognized in the late 1980's, research has increasingly focused attention on identifying the underlying causal mechanisms (reviewed in Semlitsch 2003). Hypotheses include disease, chemical contaminants, global climate change, human land-use, interactions with invasive species and over-exploitation (Collins and Storer 2003). Efforts over the last 20 years to link these hypotheses to population declines have tended to fall into two categories: 1) studies that document declines in natural populations and suggest potential causes; 2) experiments that quantify the effects of a specific factor (e.g. chemical contaminant) on growth and/or survival, usually of a single life history stage. While these studies have provided valuable insights, they typically do not offer specific conservation strategies for reversing declines. In large part, this is due to the fact that while amphibian population declines have received a great deal of attention, relatively little emphasis has been placed on understanding amphibian population dynamics (Alford and Richards 1999). This has made it difficult to assess the potential population-level consequences of the effects observed in experimental studies, or to predict the demographic response of a population to a range of possible management strategies.

Lack of demographic data for most amphibian species is a major barrier to understanding amphibian population dynamics and developing accurate demographic models (Halley et al. 1996, Biek et al. 2002). Because amphibians have a complex life cycle with aquatic egg and larval stages and terrestrial juvenile and adult stages, demographic models that incorporate this age structure require estimates of vital rates for each stage. While some parameters, such as clutch size, are relatively easy to determine, others, including survival rates of terrestrial life history stages, and age at first reproduction, are more difficult to estimate, especially for long-lived species. Additionally, studies monitoring amphibian populations rarely span a sufficient time period to capture the variation inherent in these vital rates (Meyer et al. 1998). Amphibians naturally exhibit extreme population fluctuations, with offspring production frequently varying by several orders of magnitude from one year to the next (Berven 1990, Pechmann et al. 1991, Pechmann and Wilbur 1994, Semlitsch et al. 1996, Meyer et al. 1998, Marsh 2001, Trenham et al. 2003, Taylor et al. 2006). Much of this variation is attributed to differences in temperature and rainfall among years, which can influence the number of females migrating to breeding sites (Babbitt and Tanner 2000) and can also affect larval survival to metamorphosis by determining pond volume and hydroperiod. In drought years ponds may dry completely before metamorphs have emerged, resulting in years with no recruitment (Berven 1990, Dodd 1993, Semlitsch et al. 1996, Taylor et al. 2006). Conversely, in years with high rainfall, pond volume increases, which can reduce densities of predators and competitors, resulting in higher pre-metamorph survival. High rainfall years have also been associated with higher rates of survival among adults (Berven 1990). The extreme variability of amphibian vital rates

emphasizes the importance of including environmental stochasticity in models of amphibian demography, and also highlights the need for long-term studies of natural populations in which demographic rates are quantified.

An accurate understanding of amphibian population dynamics has also been hindered by a historical focus in amphibian research on the aquatic life history stages (discussed in Biek et al. 2002, Schmidt et al. 2005). There has long been an assumption among many amphibian researchers that the larval life history stage is the primary driver of amphibian population dynamics (e.g. Wilbur and Collins 1973, Kiesecker et al. 2001). Therefore, not surprisingly, the majority of experimental research into potential causes of amphibian declines has focused to a large extent on the effects of specific stressors on larval survival and size at metamorphosis (e.g. Relyea 2003, Belden and Blaustein 2004, Boone et al. 2004, Parris and Cornelius 2004). However, sensitivity analyses conducted on recent amphibian demographic models suggest that population growth rate is least affected by pre-metamorphic vital rates (Biek et al. 2002, Vonesh and De la Cruz 2002), indicating that factors affecting survival of terrestrial life history stages may play a greater role in the growth and decline of amphibian populations than factors affecting aquatic stages.

The use of demographic models and population viability analyses in amphibian conservation research is surprisingly recent (Biek et al. 2002, Hels and Nachman 2002, Vonesh and De la Cruz 2002, Conroy and Brook 2003, Rustigian et al. 2003, Grafe 2004, Govindarajulu et al. 2005, Schmidt et al. 2005, Trenham and Shaffer 2005, Taylor et al. 2006). Population models have been widely used in developing conservation strategies for a range of other taxa over the past 20 years and can be used to achieve several

conservation goals including: 1) evaluating the extinction risk of single populations under natural conditions; 2) demonstrating the effects of specific perturbations (e.g. land use practices) on the viability of populations; 3) evaluating the potential effectiveness of multiple management options; 4) revealing relationships between life history strategies and population dynamics and; 5) elucidating the roles of environmental stochasticity and density dependence in amphibian population dynamics (Morris and Doak 2002). The accuracy of these predictions, however, depends entirely on the accuracy of the model. While the first amphibian population models were crude, based on limited demographic data from the literature and without density dependence or environmental stochasticity, they were sufficiently accurate to recognize and draw attention to the importance of the terrestrial life history stage. Recently, there has been a substantial increase in research focusing on terrestrial stage vital rates and the distribution of amphibians in the terrestrial habitat (e.g. Rittenhouse and Semlitsch in review, Semlitsch 1998, Altwegg 2003, Porej et al. 2004, Rothermel 2004, James 2005, Regosin et al. 2005, Trenham and Shaffer 2005, Crawford and Semlitsch 2006, Gamble et al. 2006, Rittenhouse and Semlitsch 2007). As more data become available, demographic models can increase in accuracy and in the range of conservation questions they are capable of answering.

In my dissertation research, I used both demographic modeling and experimental field research to evaluate the role of terrestrial habitat in the population dynamics and conservation of pond-breeding amphibians. I have focused on questions that ask how the quantity and quality of terrestrial habitat available to amphibians affects demographic rates and how these changes can affect populations. The majority of amphibian population declines in the U.S. and worldwide are occurring as the result of habitat loss

and degradation (Stuart et al. 2004). Pond-breeding amphibians clearly require aquatic breeding habitat to maintain viable populations, however, changes in terrestrial habitat quality that affect juvenile or adult survival may result in declines and increased extinction rates even when aquatic breeding habitat is unaltered (Semlitsch and Bodie 2003). Studies have documented adult amphibians regularly using terrestrial habitat at distances as far as 1 km or more away from aquatic breeding sites (Pilliod et al. 2002, Muths 2003, Bartelt et al. 2004, Gamble et al. 2006), and an analysis of data from the literature on 32 amphibian species suggests that core terrestrial habitat (the area encompassing 95% of the adults in a population) averages from 159 – 290 m away from the breeding site (Semlitsch and Bodie 2003). However, for the majority of pond breeding amphibians, the amount of terrestrial habitat loss or degradation that can be sustained while still maintaining viable populations is unknown. This information is critical to land managers, city planners, and policy makers who are attempting to balance human land use with biodiversity conservation.

In my research, I began by using data available in the literature to develop stochastic, stage-structured demographic models for two pond-breeding amphibian species, the wood frog *Rana sylvatica* and the spotted salamander, *Ambystoma maculatum* that have different life history strategies and subsequently very different population dynamics. I used these models to determine the potential effects of a range of core terrestrial habitat areas on population size and time to extinction for both species. These models allowed me to answer a specific conservation question, provide recommendations to land managers and policy makers, increase understanding of

species-specific amphibian population dynamics and identify future research priorities. These results are presented in Chapter 2.

Using the model building process to focus my research goals, I next carried out field experiments (Chapters 3 and 4) designed to improve model accuracy. While several amphibian demographic models have included aquatic density dependence (Taylor and Scott 1997, Vonesh and De la Cruz 2002, Trenham and Shaffer 2005), none have considered terrestrial density effects. However, theoretical models of complex life cycles have demonstrated that if density dependence is assumed to occur at a single stage when it in fact occurs at multiple stages, the resulting population dynamics could be fundamentally altered (Hellriegel 2000). The absence of terrestrial density effects in amphibian demographic models is most likely due to lack of data and to the emphasis on larval density dependence in the literature. Larval density has been shown to affect survival, length of larval period and size at metamorphosis in numerous studies conducted in the laboratory, in cattle tank mesocosms, and in natural ponds (reviewed in Skelly and Kiesecker 2001). Few studies have addressed the question of terrestrial density dependence in amphibians, but data from studies of breeding populations (Gill 1978, Berven 1995, Beebee et al. 1996) and experiments manipulating metamorph density (Pechmann 1995, Altwegg 2003) suggest that adult fecundity and survival can be affected. To determine functional relationships between terrestrial density and survival that could be incorporated into amphibian demographic models, I raised juvenile wood frogs and American toads at a range of densities in terrestrial enclosures and tracked growth survival and reproductive development. These results are presented in Chapter 3.

A second research focus also became clear in the model building process. While many landscape-scale studies of natural populations have correlated measures of terrestrial habitat degradation with amphibian abundance and diversity (Gibbs 1989, Babbitt et al. 2003, Egan and Paton 2004, Homan et al. 2004), few have experimentally manipulated terrestrial habitat to identify the mechanisms behind these patterns. An understanding of specific causal mechanisms and their effects on vital rates, allows the use of population viability analyses to evaluate specific conservation strategies aimed at mitigating the effects of land-use practices. To obtain data that could be used in this context, I focused on determining the effects of four different forestry practices on the survival of juvenile wood frogs and American toads. Timber harvesting has long been associated with reduced amphibian abundance and diversity (Bennett et al. 1980, Bury 1983, Ash 1988, Petranka et al. 1993, DeMaynadier and Hunter 1998), however the mechanisms behind these patterns have been the subject of debate (Petranka et al. 1993, Ash and Bruce 1994). I raised juvenile amphibians in terrestrial enclosures in replicated landscape-scale experimental forestry arrays to determine the effects of specific forestry practices on wood frog and American toad survival. I measured habitat and landscape variables within each terrestrial pen and used a regression approach to determine the relationship between survival and these variables. I then developed a set of four *a priori* candidate models to explain these relationships, and ranked the models using Akaike's information criterion. Results are presented in Chapter 4.

After carrying out field experiments to better understand the role of terrestrial density dependence (Chapter 3) and the effects of forestry practices on juvenile amphibian survival, I returned to the model building process. I incorporated these data

into a demographic model designed to evaluate the potential effects of specific forestry practices on the probability of persistence and size of local wood frog populations. I also used the model to predict the population level effects of reductions in immigration rates associated with forestry practices and to test the potential effectiveness of different management options in mitigating the effects of forestry practices. These results are presented in Chapter 5.

The combination of demographic modeling and field experiments that I used in my dissertation research is an efficient method of ensuring that amphibian conservation research focuses on factors that can have population level effects. It also allows the evaluation of specific management strategies and ensures that recommendations to land managers and policy makers are continually improved as more data become available. I review the conclusions from my research, including conservation recommendations and priorities for future research in Chapter 6.

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## **CHAPTER 2**

# **DEMOGRAPHIC CONSEQUENCES OF TERRESTRIAL HABITAT LOSS FOR POOL-BREEDING AMPHIBIANS: PREDICTING EXTINCTION RISKS ASSOCIATED WITH CORE HABITAT SIZE**

### **ABSTRACT**

Habitat loss is implicated in the decline of the majority of the 1,896 amphibian species currently threatened with global extinction. Striking a feasible balance between human land-use and habitat conservation is one of the greatest challenges in efforts to conserve biodiversity. However, the specific risks of varying amounts of habitat loss are often difficult to quantify, hindering the progress of well-informed land-use policy. Using projections of amphibian populations, we relate the amount of high quality terrestrial core habitat surrounding wetland breeding sites to the decline and risk of extinction of local amphibian populations. We show that current wetland regulations protecting 30 m or less of surrounding terrestrial core habitat are not adequate to support viable populations of pool-breeding amphibians. Our model results demonstrate that a high probability of persistence requires not only a minimum area of terrestrial core habitat, but also the maintenance of habitat quality as well as connectivity among local populations. We found that while species with a short lifespan and high fecundity are

most sensitive to habitat loss and isolation, longer lived species with lower fecundity are most sensitive to long-term habitat degradation. Our results emphasize the essential role of adequate terrestrial core habitat to the continued existence of populations of pool-breeding amphibians and offer a means of quantifying the risks associated with habitat loss and degradation.

## INTRODUCTION

While the Clean Water Act regulates the draining and filling of wetlands, federal protection of isolated wetlands was weakened by a 2001 Supreme Court ruling (*Solid Waste Agency of Northern Cook County v. U.S. Army Corps of Engineers*), and current regulations do not extend protection to the surrounding terrestrial habitat. Terrestrial habitat associated with wetlands is essential to the maintenance of wetland biodiversity (Calhoun and Klemens 2002; Findlay and Houlihan 1997), and thus to the integrity of wetland ecosystems. Therefore, some land-managers, city planners and policy makers at the state and local levels are making an effort to protect isolated wetlands and surrounding terrestrial habitat (Calhoun et al. 2005). For example, Massachusetts protects a terrestrial “buffer zone” of 30 m or less. This area begins to protect wetlands, but does not provide adequate core terrestrial habitat to maintain amphibian populations (Gamble et al. 2006; Rittenhouse and Semlitsch 2007; Semlitsch and Bodie 2003). Striking a feasible balance between human land-use and habitat conservation is challenging, and the specific risks associated with varying amounts of terrestrial habitat loss are often difficult to quantify, complicating the progress of well-informed land-use policy.

Habitat loss is implicated in the decline of the majority of the 1,896 amphibian species currently threatened with global extinction (Stuart et al. 2004). Amphibians that breed in temporary wetland pools require not only aquatic breeding habitat, but also terrestrial foraging and overwintering habitat to maintain viable populations. An analysis of data from the literature on 32 amphibian species suggests that core terrestrial habitat (the area encompassing 95% of the adults in a population) averages from 159 – 290 m away from the breeding site (Semlitsch and Bodie 2003), and several additional studies document adult amphibians regularly using terrestrial habitat at distances as far as 1 km or more (Bartelt et al. 2004; Gamble et al. 2006; Muths 2003; Pilliod et al. 2002).

Recent demographic models of amphibian population dynamics have demonstrated that population growth in several species is extremely sensitive to changes in terrestrial juvenile and adult survival rates (Biek et al. 2002; Vonesh and De la Cruz 2002). Additionally, numerous landscape scale studies correlate the amount of forest cover within the core terrestrial habitat area and the presence or absence of many amphibian species (Guerry and Hunter 2002; Herrmann et al. 2005; Homan et al. 2004; Porej et al. 2004; Rubbo and Kiesecker 2005). These findings suggest that even when aquatic habitat is protected, degradation and loss of terrestrial habitat are likely to lead to amphibian population declines and extinctions.

Maintaining extensive amounts of pristine upland habitat surrounding wetlands is not feasible in many human-dominated landscapes. For land managers balancing multiple management objectives (e.g., timber harvest, recreation opportunities, and biodiversity conservation), or for town planners regulating development, it is important to identify the specific risks and benefits associated with the maintenance of different

amounts of upland habitat. However, scant data on the terrestrial ecology of amphibians limit specific policy recommendations as to the minimum amount of terrestrial core habitat necessary to maintain viable amphibian populations. Currently, minimum terrestrial core habitat recommendations based on adequate field data and demographic models have been made only for the federally threatened California tiger salamander, *Ambystoma californiense* (Trenham and Shaffer 2005). Similar recommendations are not available for pool-breeding species in many parts of the U.S. where regulations protecting wetland habitat are currently being revised.

To evaluate the population level consequences of reductions in terrestrial habitat for pool-breeding amphibians, we developed stochastic matrix population models for two amphibian species, the wood frog (*Rana sylvatica*) and spotted salamander (*Ambystoma maculatum*), using demographic data available in the literature. We chose these species because both are forest-dependent and breed in seasonal wetland pools throughout the north-eastern U.S. However, differences in the life history strategies and population dynamics of the two species may result in differing responses to terrestrial habitat loss.

Through model simulations, we predicted the decline and risk of extinction of wood frog and spotted salamander populations resulting from truncation of terrestrial habitat surrounding wetland breeding sites. We ran simulations for both species to determine the population size and probability of persistence resulting from a range of terrestrial habitat radii. We also ran simulations to determine how these predictions are influenced by reductions in habitat quality within the remaining terrestrial habitat and by the degree of connectivity among local populations.

## METHODS

### *Study species*

Wood frogs are short-lived, with most individuals breeding only once or twice in a lifetime (Berven 1990). Males typically reach reproductive maturity within a year and females in 1 – 2 years. Wood frog clutch sizes are large, containing several hundred to over a thousand eggs (Berven 1988). Successful metamorphosis is often tied to rainfall patterns, with catastrophic mortality occurring in years of low rainfall when pools dry before metamorphs emerge, and with high rainfall years allowing metamorph production in the tens of thousands (Berven 1990). These boom and bust years lead to large fluctuations in adult wood frog population sizes. Spotted salamanders are a longer-lived amphibian species and typically breed 4 or more times in a lifetime (Husting 1965). Females do not reach reproductive maturity until around 4 years of age and may take as long as 7 years in far northern populations (Flageole and Leclair Jr. 1992; Wilbur 1977). Clutch sizes are much smaller in spotted salamanders than in wood frogs, with females laying approximately 100 – 300 eggs (Shoop 1974). Females may occasionally skip a year of breeding, possibly due to weather conditions or an inability of the individual to acquire sufficient resources for reproduction (Blackwell et al. 2004). Survival from egg to metamorphosis can vary dramatically from year to year as in wood frogs, but because adults are longer-lived, adult population sizes tend to fluctuate less in spotted salamander populations than in wood frog populations.

### *Model structure and parameterization*

**Wood Frog** – We developed an age-based stochastic demographic matrix model for the wood frog consisting of 4 age classes; 1) Pre-metamorph (egg and larval stages); 2) One-

year-old; 3) Two-year-old and 4) Three-year-old (Fig. 1A). The model tracks only females in the population because females lay only one clutch a year whereas males are capable of fertilizing multiple clutches and are therefore not considered limiting to population growth.

Model parameterization was based on data reported in Berven (1990) as part of a 7-year study of a wood frog population in Beltsville, Maryland. Egg survival to metamorphosis varied drastically among years in this population and was positively correlated with rainfall. We used data from the Beltsville weather station (noaa.gov) to determine the functional relationship between spring rainfall (in.) and the probability of egg survival to metamorphosis for the years 1976 – 1980 ( $y = 0.0088x - 0.062$ ;  $r^2 = 0.60$ ). We used this relationship along with weather station data from 1950 – 2005 to estimate the range and frequencies of rates of egg survival to metamorphosis, thereby incorporating environmental stochasticity into model projections (Table 1). We used 3 values for metamorph survival to one year, including the mean, the mean + 1 standard deviation, and the mean – 1 standard deviation, reported in Berven (1990). In model projections the mean value for metamorph survival was drawn randomly with a probability of 0.50 and the other 2 values were each drawn with a probability of 0.25 (Table 1).

We calculated one-year-old survival, two-year-old survival and fecundity values based on life table data from 4 cohorts in Berven (1990), giving 4 possible values for each of these parameters (Table 1). As we ran the model projections, 1 of these 4 values was drawn at random in each year, with the highest and lowest values each drawn with a probability of 0.15 and the two moderate values each drawn with a probability of 0.35.

Although matrix elements were drawn at random, we assumed that one-year-old and two-year-old survival are highly correlated within years, therefore these values were drawn in pairs so that, for example, a year with high one-year-old survival would also be a year with high two-year-old survival. Before running model projections in which habitat area was reduced, we calculated the stochastic log growth rate of the parameterized model to ensure that we began with a population that was neither growing nor declining.

**Spotted salamander** – We built a stochastic stage-based female-only matrix model for the spotted salamander using data from the literature. When possible we based our estimates on populations from the north-eastern United States because demographic rates can vary geographically. The model consisted of three stages; 1) Pre-metamorph; 2) Juvenile and 3) Mature adult (Fig. 1B). Estimates of survival to metamorphosis were based on a five-year study of spotted salamanders in two temporary pools in Massachusetts (Shoop 1974). As in the wood frog model, we used weather station data (1906 – 2005; East Milton Blue Hill Observatory, Norfolk County; noaa.gov) to determine the relationship between spring rain (mm) and probability of survival to metamorphosis ( $y = 8^{-5}x - 0.0298$ ;  $r^2 = 0.97$ ) and used the predicted survival rates and frequencies to simulate environmental stochasticity in the model (Table 2). Data on survival of metamorphs to juveniles were not available for populations in the north-east. Our estimates are based on a study of spotted salamander metamorphs raised in enclosures in forest habitat in Missouri (Rothermel and Semlitsch 2006). We used four values for metamorph survival which were drawn at random in proportions based on the frequencies reported in the study (Table 2). Annual juvenile survival is a difficult parameter to estimate because most survival estimates for spotted salamanders are based

on data from adults that return regularly to breeding sites, whereas juveniles are far more difficult to relocate on an annual basis. Our estimate of 0.76 for juvenile survival was inferred by determining the value required to yield a stochastic log growth rate of 1 after all other matrix elements had been parameterized using literature data. This estimate is reasonable assuming that juvenile survival is likely to be much higher than metamorph survival, but not as high as adult survival rates. Our estimates of adult survival were based on two studies of populations in the north-east (Husting 1965; Whitford and Vinegar 1966). From these studies we used 3 possible values for adult survival that were drawn at random in equal proportions in the model projections (Table 2). The annual probability of transition from juvenile to reproductively mature adult is based on Wilbur's (1977) estimate that females reach maturity in 3-5 years. The model drew randomly in equal proportions from 3 possible values for this transition probability (Table 2). Fecundity in our model is a function of clutch size, breeding frequency, 0.50 (with the assumption that half of the clutch is female), and adult survival (because the model is a post-breeding model and individuals must survive to the next year to breed). Our estimates of fecundity are based on an average clutch size of 224 (Shoop 1974), the value of adult survival randomly selected in the model projections, and randomly selected breeding frequencies ranging from 0.75 to 0.90 (Blackwell et al. 2004; Whitford and Vinegar 1966).

### ***Estimating distribution of individuals in the terrestrial habitat***

To predict the effects of loss of terrestrial core habitat on amphibians, it is essential to know how individuals in the population are distributed spatially. We used univariate kernel density estimates of space-use for frogs and salamanders reported in (Rittenhouse

and Semlitsch 2007) to estimate the proportion of individuals in the population affected by a range of terrestrial core habitat radii (Table 3). These estimates are based on 13 radio telemetry studies of adult amphibians breeding in wetland habitats. Distributions for both frogs and salamanders peak near the pond and decline at greater distances, however, frogs generally use terrestrial habitat at far greater distances than do salamanders. In our simulations we considered 100% of wood frogs to occur within 1000 m of the breeding pool and 100% of spotted salamanders to occur within 290 m of the breeding pool. We ran simulations for wood frogs with 9 different terrestrial core habitat radii ranging from 30 – 1000 m and for spotted salamanders with 8 terrestrial core habitat radii ranging from 5 – 290 m (Table 3). For each species these ranges affected from 0 – 93% of individuals in the population (Table 3).

### ***Model projections***

Initial wood frog and spotted salamander population sizes were drawn at random in specified proportions from a range of population sizes based on surveys of 124 ponds in Rhode Island (Egan and Paton 2004). Carrying capacity is included in the model as a cap on the number of females per area of remaining suitable terrestrial habitat. We based estimates of maximum breeding population size on data from Egan and Paton's (2004) wood frog and spotted salamander egg mass counts in 124 ponds in Rhode Island. Wood frog carrying capacity was set at a total of 1033 adult females and spotted salamander carrying capacity at 250 adult females. These values were used in the model when sufficient terrestrial core habitat was available to encompass 100% of the adult breeding population, and were reduced proportionally according to the number of individuals affected by reductions in terrestrial core habitat radii (Table 3).

For each model simulation we ran 30 iterations. Each iteration consisted of 5,000 replications in which the population was projected forward 20 years. Model output included extinction probabilities for each year (mean from the 30 iterations) and mean and median adult female population sizes at 20 years. Populations were considered extinct when less than 1 adult female remained in the population. All model simulations were run with the assumption that individuals outside of the radius of suitable terrestrial habitat die in the first year that habitat area is lost, and that in subsequent years carrying capacity is reduced. We ran three sets of model simulations that differed in their assumptions regarding degree of habitat degradation and rates of immigration.

***1) Simulations assuming no habitat degradation or immigration***

This first set of model projections was run with the assumption that habitat quality within the radius of remaining forested terrestrial habitat is not degraded (e.g. from edge effects), and therefore adult survival rates within this area were not reduced. This assumes that the remaining terrestrial habitat includes areas suitable for both foraging and overwintering. These simulations also assume that loss of surrounding forested habitat results in isolation of the population, eliminating the possibility of immigration or recolonization.

***2) Simulations assuming a range of habitat degradation***

Because there are not sufficient data to determine the effects of habitat degradation on terrestrial survival rates, or to estimate the effect of reductions in specific habitat types (i.e. over-wintering vs. foraging) on terrestrial survival rates in the remaining population, we ran simulations for a range of habitat degradation scenarios, with survival rates of all terrestrial life history stages reduced in increments of 5% from 0

– 25%. This allowed us to determine the sensitivity of extinction probabilities to reductions in terrestrial survival rates for both wood frogs and spotted salamanders.

### ***3) Simulations assuming a range of immigration frequencies in wood frog populations***

The combination of extremely variable recruitment and short lifespan of wood frogs results in a high probability of local extinction, suggesting that these populations may be dependent on immigration and recolonization for long term persistence, whereas longer-lived spotted salamanders are less likely to experience local extinctions. To test the effects of immigration on wood frog extinction probabilities, we ran simulations with annual probabilities of successful immigration ranging from 0.10 to 0.5 (approximately once every 10 years to once every 2 years). During model projections, 5 one-year-olds were added to the population vector in years that were randomly selected as having successful immigration.

## **RESULTS**

### ***Simulations assuming no habitat degradation or immigration***

Reduction in terrestrial core habitat area resulted in increased extinction probabilities and decreased mean and median population sizes for both wood frogs and spotted salamanders (Figs. 2 and 3). Extinction probabilities for wood frogs were higher than for spotted salamanders when sufficient terrestrial core habitat was available to encompass 100% of the population (1000m radius for wood frogs and 290 m for spotted salamanders). Wood frog populations had an 11% probability of extinction within 20 years compared to only a 0.02% probability of extinction for spotted salamanders. However, spotted salamander extinction probabilities were much higher (45%) than those

of wood frogs (24%) when terrestrial habitat radii were reduced so that 93% of the population was affected. The two species also differed in that extinction probabilities increased steadily over time for wood frogs across the entire range of terrestrial core habitat radii, but were relatively constant over time for spotted salamanders (Fig. 2). Wood frog and salamander population sizes both responded similarly, however, with mean and median population sizes declining steadily with reductions in terrestrial core habitat area (Fig. 3).

### ***Simulations assuming a range of habitat degradation***

In model simulations that included reductions in terrestrial survival rates of individuals within the forested habitat radius, extinction probabilities increased for both species, but at a far greater rate for spotted salamanders than for wood frogs (Fig. 4). With only a 5% reduction in terrestrial survival rates of spotted salamanders, extinction probabilities quadrupled for populations with a 20 m radius of terrestrial core habitat and increased over 78 times for populations with 290 m of terrestrial core habitat. When terrestrial survival rates were reduced by 25%, all salamander populations reached extinction within 20 years. The same 25% reduction in terrestrial survival rates in wood frog populations only slightly more than doubled extinction probabilities, with at most a 58% probability of extinction.

### ***Simulations assuming a range of immigration frequencies in wood frog populations***

Wood frog extinction probabilities were substantially reduced in simulations that allowed successful immigration (Fig. 5). Immigration occurring even as infrequently as once every 7 years resulted in a 50% reduction in wood frog extinction probabilities within 20 years. Extinction probabilities were reduced by similar proportions for

simulations with a 165 m of terrestrial core habitat and were reduced by an even greater proportion for simulations with 30 m of terrestrial core habitat. In these simulations, immigration with a frequency of once every 8 years was sufficient to reduce extinction probabilities by 50%, and successful immigration with a frequency of every 3<sup>rd</sup> year reduced extinction probabilities by 80%. However, median population sizes in the 30 m habitat simulations were still drastically reduced, with even the most frequent immigration (once every 2 years) still resulting in population reductions of over 90% (Fig. 5). Median population sizes in the simulations with a 1000 m and 165 m habitat radii, however increased 4 to nearly 7-fold depending on the frequency of successful immigration.

## **DISCUSSION**

Our model simulations predict increased risk of decline and extinction for wood frog and spotted salamander populations when terrestrial habitat surrounding breeding sites is reduced. When terrestrial habitat is reduced to 30 m or less and we assume survival is only reduced by 5% (an extremely low reduction), our results indicated spotted salamander declines of 80% in median population size and resulted in an 18% probability of extinction within 20 years. For wood frogs, the consequences of this buffer width were even greater, with declines of 94% in median population size and a 29% probability of extinction within 20 years. It is clear from these results that terrestrial buffer widths of 30 m or less around breeding pools do not provide adequate terrestrial core habitat to maintain viable populations of wood frogs or spotted salamanders.

Although pool-breeding amphibians clearly require more than 30 m of terrestrial habitat around breeding sites, the necessary area of terrestrial core habitat will depend on

the goals of a particular conservation policy or land management plan. For example, a population of spotted salamanders may have a relatively low probability of extinction with a terrestrial core habitat radius of 50 m assuming the quality of the habitat remains high, but the size of the population will likely be reduced to less than half its original size. With a 50 m buffer, the majority (78%) of wood frog populations are predicted to persist, albeit with median population sizes reduced by 89%. The resulting reduction in population size for both species combined would drastically diminish the role of the populations in the surrounding terrestrial ecosystem by decreasing the volume of nutrients transferred from the aquatic to terrestrial habitat and by reducing the prey base available to amphibian predators (Semlitsch 2003). This outcome may be adequate if the goal is a low probability of population extinction, but may not be acceptable to a land manager or policy maker whose goal is the maintenance of ecosystem function.

To maintain populations of spotted salamanders with a 95% probability of persistence over 20 years, our models indicated that a terrestrial core habitat radius of between 100 – 165 m (330 – 540 ft) is required, assuming sufficient habitat quality is maintained to prevent reductions in terrestrial survival rates of more than 5%. To ensure high probabilities of persistence, the area within 165 m of the breeding site should be considered ‘core habitat’ and an additional ‘buffer zone’ around this area should be in place to ensure that the core habitat quality remains high (Semlitsch and Jensen 2001). In addition, the importance of high quality terrestrial core habitat for the maintenance of spotted salamander populations was emphasized by their high sensitivity to changes in terrestrial survival rates. Even with sufficient terrestrial core habitat to encompass 100% of the adult population, spotted salamanders in our simulations experienced extinction

probabilities of nearly 50% when terrestrial survival rates were reduced by 15%.

Therefore wetland policies such as the recent amendments to Massachusetts' Wetlands Protection Act that require a 100 ft. buffer zone around wetlands, but allow construction within the outer 50 ft and as much as 40% impervious surface, are likely eroding habitat quality within wetland buffer zones to a degree that local extinctions of salamander populations are highly likely.

For wood frogs, our models indicated that maintaining a 95% probability of persistence over 20 years requires not only adequate terrestrial core habitat, but also a sufficient degree of connectivity with other breeding populations. Extinction probabilities within 20 years were over 5% for wood frogs even with a habitat radius that encompassed the entire population and with high quality habitat that did not reduce adult survival. This result indicates that wood frog populations are highly prone to stochastic extinction and are dependent on re-colonization for long term persistence. Therefore, isolating wood frog populations from the possibility of re-colonization will likely prevent long-term population persistence. Our model results are supported by landscape scale studies of amphibian populations suggesting that isolated populations of wood frogs are highly susceptible to stochastic extinction (Gibbs 1989). When we included successful immigration in our model simulations, extinction probabilities were substantially reduced and median population sizes increased. For wood frog populations with a terrestrial core habitat radius of 165 m and with a frequency of successful immigration once every 4 years, simulations resulted in a probability of persistence of over 95%. Current policies regulating development near wetlands do not address the issue of maintaining connectivity among small wetlands. For wood frogs and other amphibian species with

similar demographic traits, the opportunity for successful immigration is essential to the maintenance of viable populations.

Our model results support the conservation recommendations of previous studies that emphasize the importance of sufficient high quality terrestrial core habitat and connectivity for the maintenance of pool-breeding amphibian populations. Numerous landscape scale studies have demonstrated strong relationships between the presence or absence of pool-breeding amphibian species and the amount of forest cover in the terrestrial landscape surrounding amphibian breeding sites (Findlay and Houlihan 1997; Gibbs 1989; Hecnar and M'Closkey 1996; Porej et al. 2004). While it may not be feasible to maintain a 165 – 200 m radius of high quality terrestrial core habitat around all amphibian breeding sites, local governments can prioritize and protect wetlands of high ecological significance. Conservation strategies such as those outlined in the Best Development Practices described by Calhoun et al. (2005), allow for the preservation of high quality wetlands and adjacent habitat while allowing development to proceed near degraded wetlands that no longer provide usable wildlife habitat.

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**Table 1.** Parameter estimates and frequencies at which each estimate was drawn during wood frog matrix population model projections. Notation in parentheses corresponds with survival (s) and fecundity (f) shown in figure 1.

<b>Parameter</b>	<b>Estimates</b>	<b>Frequency</b>
<b>Egg survival to metamorphosis (<math>s_1</math>)</b>	0	0.058
	0.013	0.327
	0.033	0.308
	0.053	0.135
	0.073	0.115
	0.090	0.058
<b>Metamorph survival to one year (<math>s_2</math>)</b>	0.25	0.250
	0.38	0.500
	0.50	0.250
<b>1-year-old survival to 2-year-old (<math>s_3</math>)</b>	0.14	0.150
	0.18	0.350
	0.21	0.350
	0.61	0.150
<b>2-year-old survival to 3-year-old (<math>s_4</math>)</b>	0.08	0.150
	0.09	0.350
	0.12	0.350
	0.23	0.150
<b>Fecundity of pre-metamorphs (<math>f_1</math>)</b>	0	0.150
	0.02	0.350
	0.10	0.350
	0.26	0.150
<b>Fecundity of 1-year-old (<math>f_2</math>)</b>	40.88	0.150
	50.70	0.350
	71.50	0.350
	229.06	0.150
<b>Fecundity of 2-year-old (<math>f_3</math>)</b>	29.43	0.150
	30.08	0.350
	43.72	0.350
	68.80	0.150

**Table 2.** Parameter estimates and frequencies at which each estimate was drawn during spotted salamander population projections. Notation in parentheses corresponds with survival (s), fecundity (f) and transition probabilities (p) shown in figure 1.

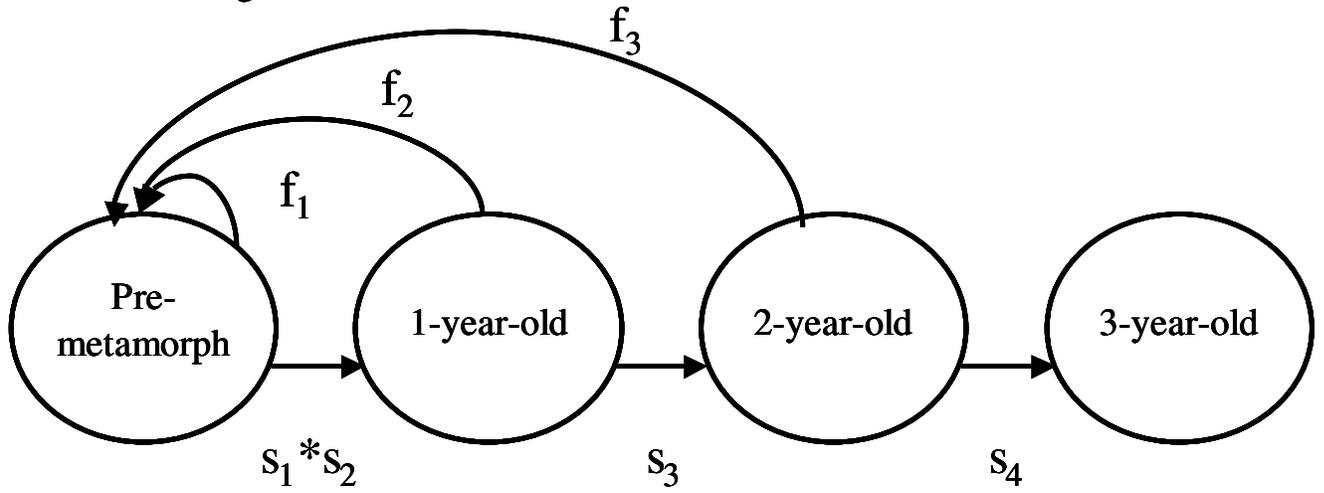
<b>Parameter</b>	<b>Estimate</b>	<b>Frequency</b>
<b>Pre-metamorph survival (<math>s_1</math>)</b>	0	0.05
	0.025	0.10
	0.045	0.29
	0.065	0.26
	0.085	0.15
	0.150	0.08
	0.125	0.07
<b>Metamorph survival to juvenile (<math>s_2</math>)</b>	0	0.37
	0.08	0.13
	0.17	0.37
	0.025	0.13
<b>Juvenile survival (<math>s_3</math>)</b>	0.76	1
<b>Adult survival (<math>s_4</math>)</b>	0.7	0.33
	0.8	0.34
	0.9	0.33
<b>Transition from juvenile to adult (<math>p_1</math>)</b>	0.33	0.33
	0.25	0.34
	0.20	0.33
<b>Clutch size</b>	224	1
<b>Breeding frequency</b>	0.75	0.25
	0.89	0.50
	0.90	0.25

**Table 3.** Terrestrial habitat radii used in model projections for wood frogs and spotted salamanders. We report the cumulative sum of density estimates from the wetland to a given radius (Cumulative Density), extracted from univariate kernel density estimates published in Rittenhouse and Semlitsch (2007). These estimates were used to determine the proportion of the population of frogs and salamanders using terrestrial habitat within a given radius of the wetland as well as reductions in terrestrial carrying capacity.

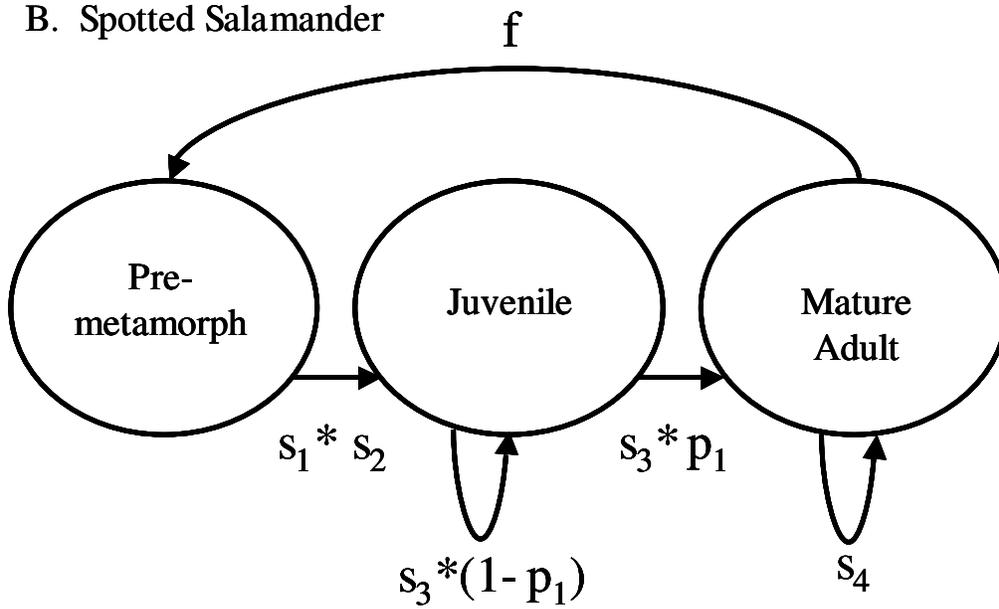
	<b>Terrestrial Habitat Radii (m)</b>	<b>Cumulative Density</b>	<b>Proportion of Population</b>	<b>Carrying Capacity</b>
<b>Frogs</b>	30	0.0258	0.074	76
	50	0.0453	0.129	133
	100	0.0986	0.281	290
	165	0.1627	0.463	479
	290	0.2438	0.694	717
	340	0.2630	0.749	774
	500	0.3046	0.867	896
	750	0.3403	0.969	1001
	1000	0.3512	1.000	1033
<b>Salamanders</b>	5	0.0268	0.073	11
	10	0.0487	0.132	20
	20	0.0949	0.257	38
	30	0.1351	0.365	55
	50	0.1887	0.510	77
	100	0.2628	0.710	107
	165	0.3251	0.879	132
	290	0.3684	0.996	149
	1000	0.3699	1	150

**Figure 1.** Life cycle diagrams illustrating the structure of the wood frog (A) and spotted salamander (B) matrix models with stage and age specific rates of survival ( $s$ ), fecundity ( $f$ ) and transition ( $p$ ).

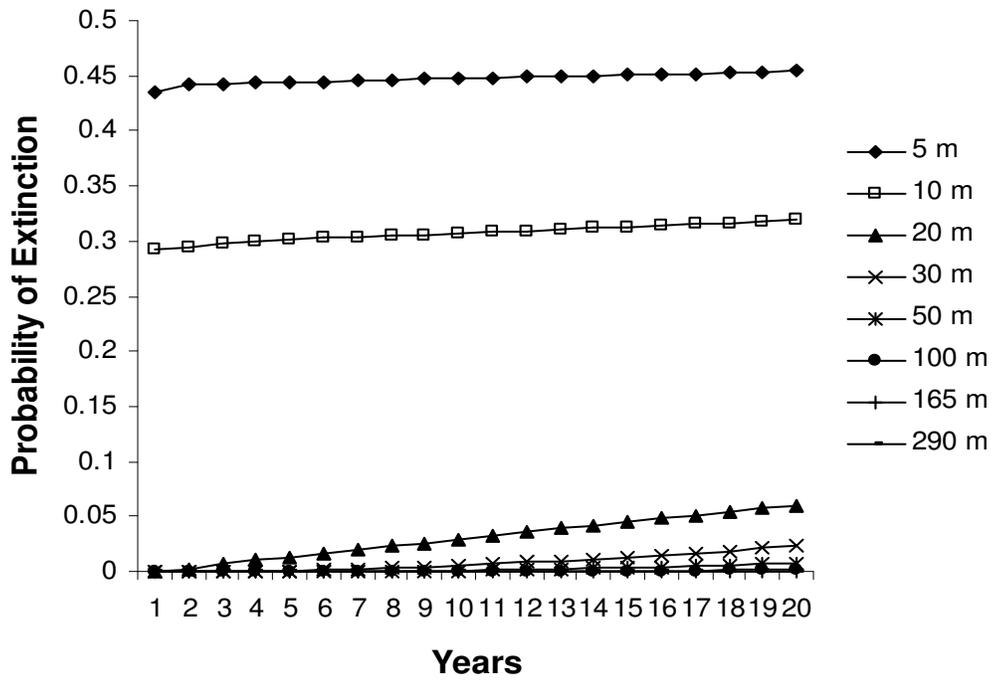
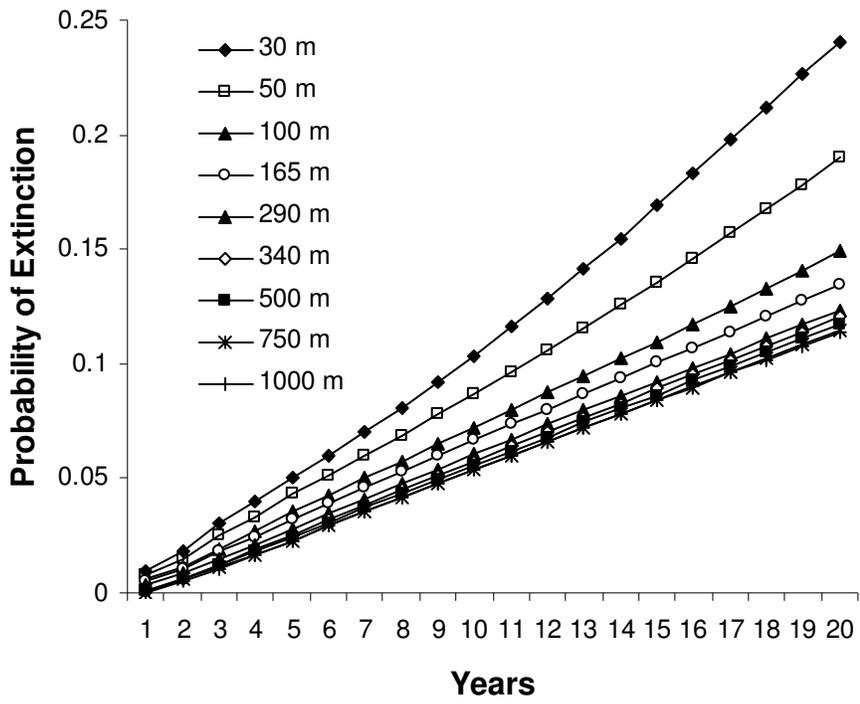
A. Wood Frog



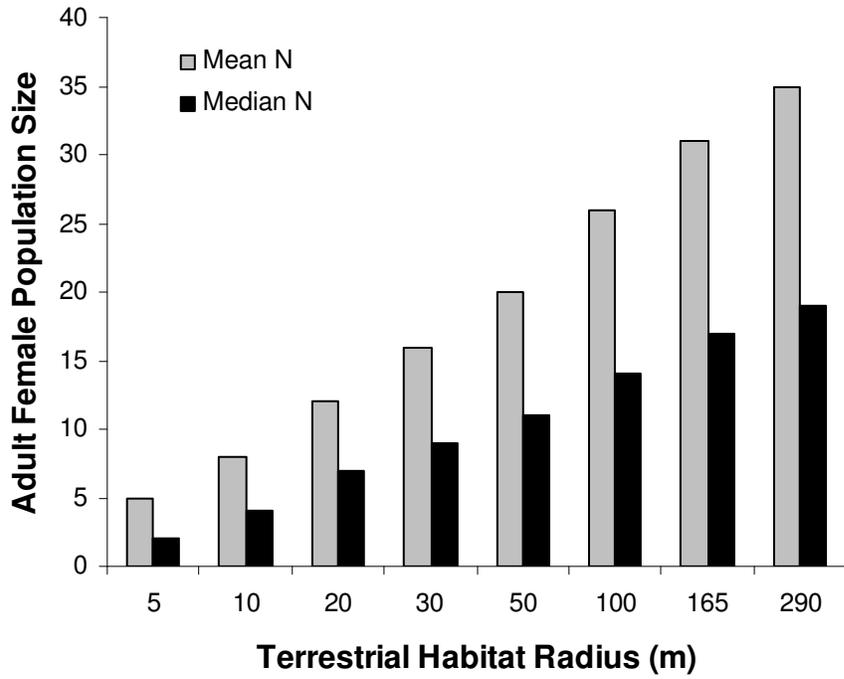
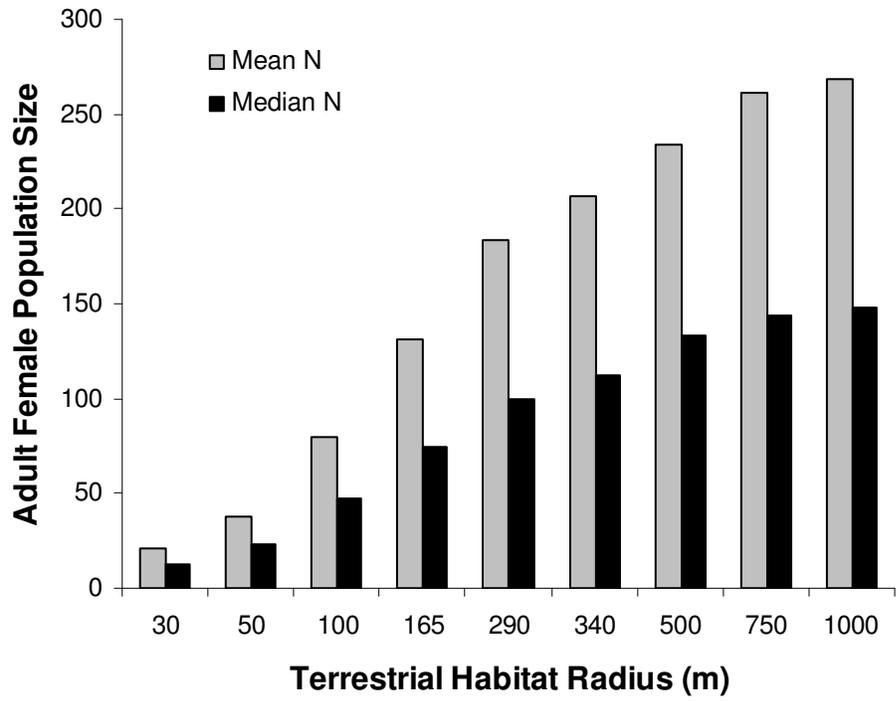
B. Spotted Salamander



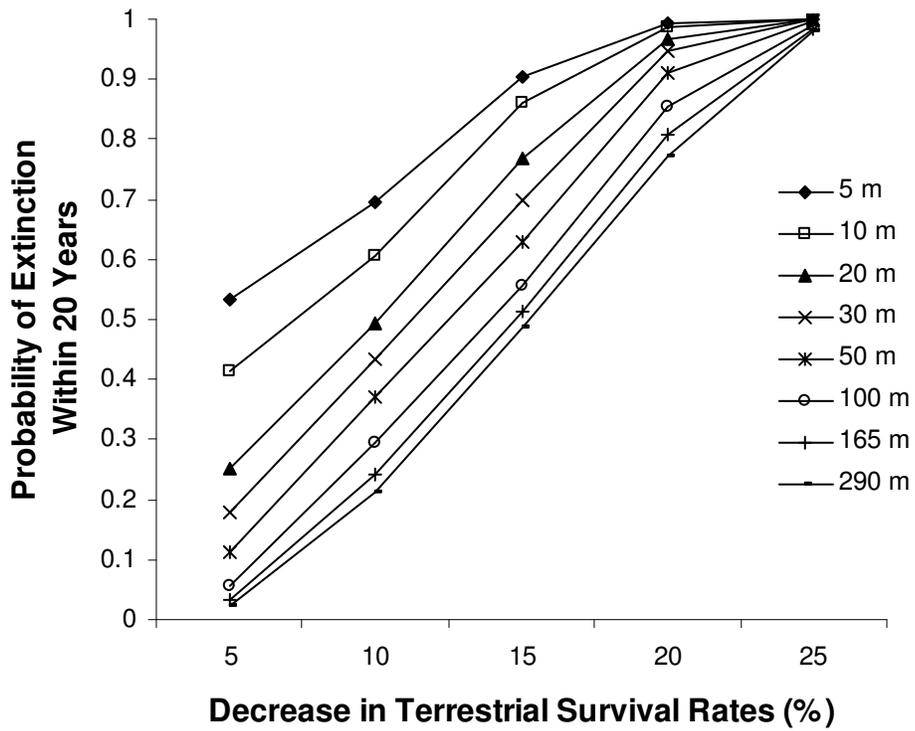
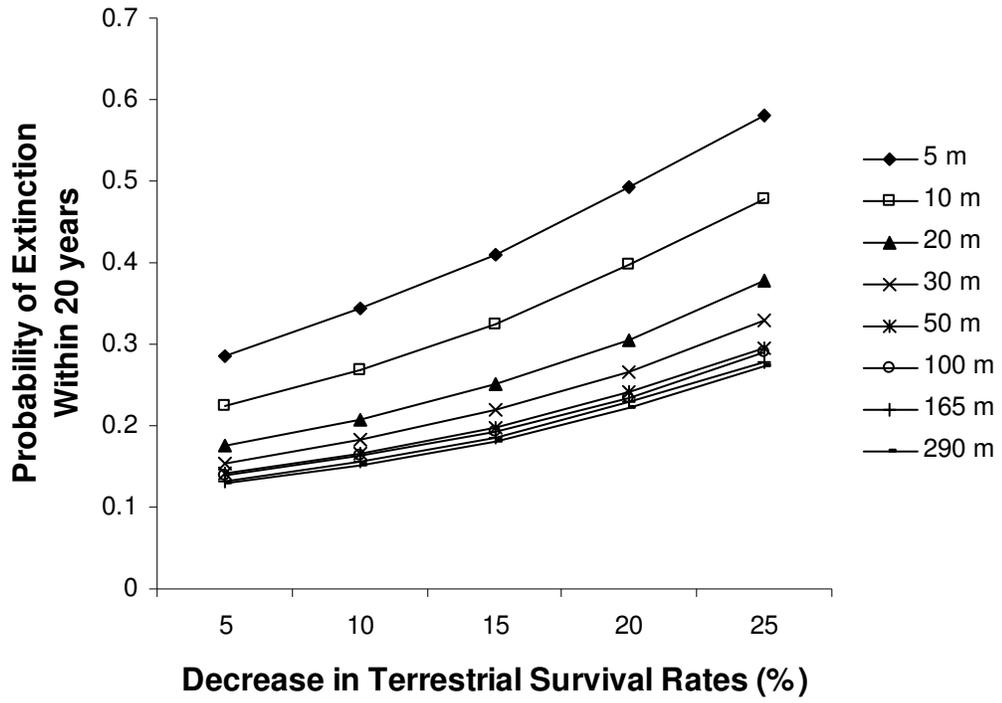
**Figure 2.** Results of model simulations predicting the probability of extinction within 20 years for wood frog populations with terrestrial core habitat radii ranging from 30 – 1000 m (A) and for spotted salamander populations with terrestrial core habitat radii ranging from 5 – 290 m (B). Model simulations assumed mortality of all individuals outside of the suitable terrestrial core habitat radius in the first year and a reduction in carrying capacity in subsequent years.



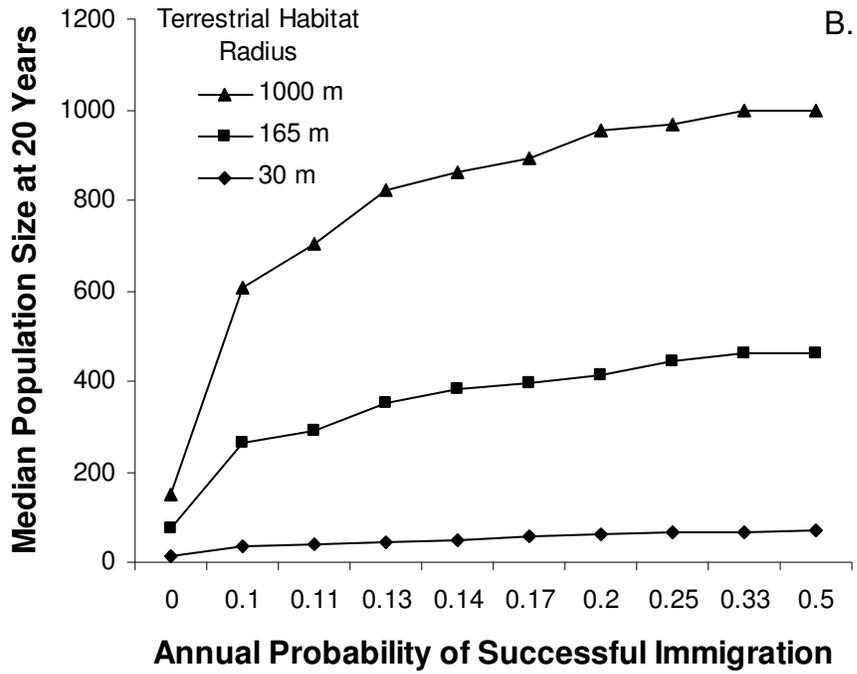
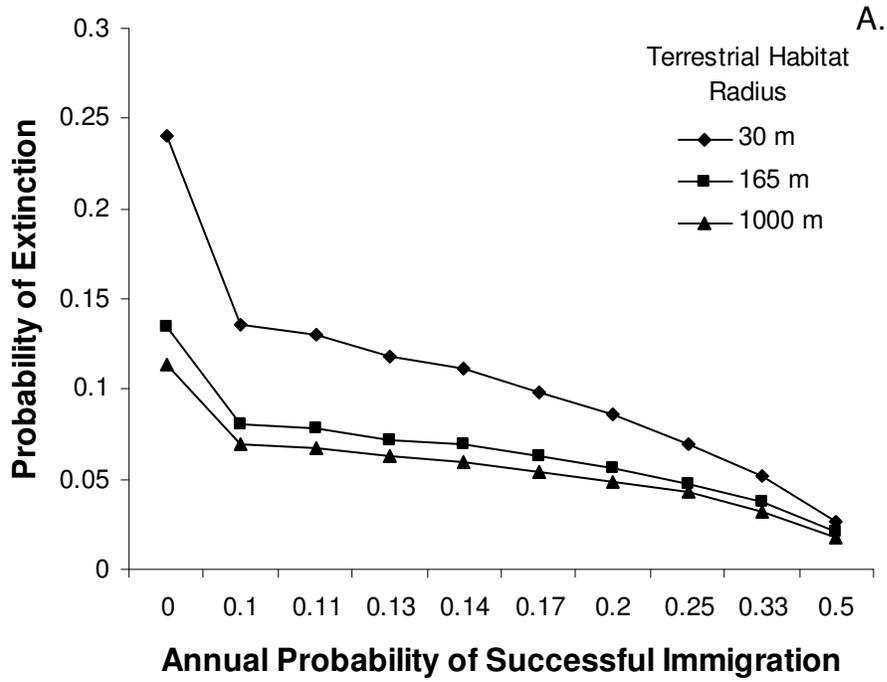
**Figure 3.** Mean and median adult female population sizes for wood frogs (A) and spotted salamanders (B) after 20 years of reduced terrestrial core habitat with terrestrial core habitat radii ranging from 20 – 1000 m for wood frogs and – 290 m for spotted salamanders.



**Figure 4.** Increases in probability of extinction of wood frog (A) and spotted salamander (B) populations within 20 years when habitat loss is accompanied by reductions in terrestrial survival rates for individuals in the remaining terrestrial core habitat.



**Figure 5.** Effects of the frequency of successful immigration of wood frogs on the probability of extinction within 20 years (A) and on the median population size after 20 years (B). Results are shown for a range of terrestrial core habitat radii identified in the legend.



## CHAPTER 3

### DENSITY DEPENDENCE IN THE TERRESTRIAL LIFE HISTORY STAGE OF TWO ANURANS

#### ABSTRACT

Populations of species with complex life cycles have the potential to be regulated at multiple life history stages. However, research tends to focus on single stage density-dependence, which can lead to inaccurate conclusions about population regulation and subsequently hinder conservation efforts. In amphibians, many studies have demonstrated strong effects of larval density and have often assumed that populations are regulated at this life history stage. However, studies examining density regulation in the terrestrial stages are rare, and the functional relationships between terrestrial density and vital rates in amphibians are unknown. We determined the effects of population density on survival, growth and reproductive development in the terrestrial stage of two amphibians by raising juvenile wood frogs (*Rana sylvatica*) and American toads (*Bufo americanus*) at 6 densities in terrestrial enclosures. Density had strong negative effects on survival, growth and reproductive development in both species. We fitted *a priori* recruitment functions to describe the relationship between initial density and the density of survivors after one year, and determined the functional relationship between initial density and mass after one year. Animals raised at the lowest densities experienced growth and survival rates over twice as great as those raised at the highest density. All female wood frogs in the lowest density treatment showed signs of reproductive

development, compared to only 6% in the highest density treatment. Female American toads reached minimum reproductive size only at low densities, and male wood frogs and American toads reached maturity only in the 3 lowest density treatments. Our results demonstrate that in the complex life cycle of amphibians, density in the terrestrial stage can reduce growth, survival and reproductive development and may play an important role in amphibian population regulation. We discuss the implications of these results for population regulation in complex life cycles and for amphibian conservation.

## **INTRODUCTION**

Populations of organisms with complex life cycles in which adult and juvenile stages occupy different habitat types have the potential to be regulated at one or multiple life history stages (Hellriegel 2000; Rodriguez 1988; Semlitsch et al. 1996; Wilbur 1980). Regulation occurs when the density of conspecifics reduces the growth, survival or fecundity of individuals, slowing the growth rate of the population. In stage-structured populations, changes in the vital rates of some stages often have a much greater effect on the growth rate of the population than others (Benton and Grant 1999). Small changes in the vital rates of these sensitive stages can reduce the population growth rate to a far greater degree than much larger changes in the vital rates of less sensitive stages.

Among organisms with complex life histories, stages with the greatest variability in vital rates tend to attract our attention and we often assume that this variability is the mechanism regulating populations (e.g. larval survival in amphibians and recruitment in reef fishes). However, across a broad range of organisms with stage-structured populations, there is a strong negative relationship between the variability of a stage

specific vital rate and its effect on population growth rate (Pfister 1998). This relationship implies that less variable vital rates, which are often the least studied among organisms with complex life histories, have the greatest potential to regulate populations. Although this is seemingly counterintuitive, evolutionary theory suggests there should be strong selection against variability in the vital rates that bound population size and thereby reduce extinction risk (Vucetich et al. 2000).

Making inaccurate assumptions about the stage at which populations are regulated may not only hinder our understanding of the dynamics of stage-structured populations, but also our ability to conserve them by misdirecting management strategies to focus on the life history stages that are the least likely to reverse population declines (Crouse et al. 1987). With habitat loss and alteration as the leading cause of species extinction, organisms with complex life cycles that require multiple habitat types are at increased risk (Semlitsch 2003). Amphibians are a prime example, with widespread population declines and one-third of species threatened globally (Stuart et al. 2004). Amphibian research and conservation strategies have overwhelmingly focused on aquatic life history stages and the protection of aquatic breeding habitat (Gamble et al. 2006; Rittenhouse and Semlitsch 2007). While aquatic habitat is clearly essential to the viability of these populations, adequate protection of terrestrial habitat may be equally important. A better understanding of the life history stages regulating these populations will aid in the development of demographic models capable of assessing the quantity and quality of terrestrial and aquatic habitat necessary to maintain viable populations, thus allowing the implementation of well informed management strategies to reverse population declines.

The complex life history of most amphibians consists of an aquatic larval stage followed by terrestrial juvenile and adult stages (Semlitsch and Bodie 2003). Density dependence in the larval stage of amphibians has been clearly demonstrated in numerous laboratory, mesocosm, and pond enclosure experiments (reviewed in Skelly and Kiesecker 2001), with the majority documenting a strong negative relationship between larval density and vital rates including survival, growth rate and size at metamorphosis. The consistency of these results often leads to the assumption that amphibian population regulation occurs in the larval stage. Several studies have documented larval density effects in natural amphibian populations (Newman 1987; Smith 1983; VanBuskirk and Smith 1991); however, few studies have examined the influence of these effects on the growth rate of the population as a whole. Sensitivity analyses conducted on demographic models for a range of amphibian species demonstrate that pre-metamorphic vital rates have the least effect on population growth rate (Biek et al. 2002; Vonesh and De la Cruz 2002), suggesting that terrestrial stage vital rates may play a greater role in population regulation than aquatic vital rates.

Studies of terrestrial density are rare in amphibians, but experimental manipulations have demonstrated density effects on growth in juvenile *Bufo marinus* (Cohen and Alford 1993), *Rana lessonae* (Altwegg 2003), and *Gastrophryne carolinensis* (Pechmann 1994). However, the functional relationships between terrestrial density and adult vital rates are unknown, making it difficult to incorporate terrestrial density effects into models of amphibian demography. To determine the functional relationships between terrestrial density and survival, growth and reproductive development in two amphibian species, we raised juvenile wood frogs (*Rana sylvatica*) and American toads

(*Bufo americanus*) at 6 densities in 48 terrestrial enclosures. Densities ranged from 1 – 10 metamorphs/m<sup>2</sup>. We tracked individual growth and survival over one year. At the end of one year animals were removed from enclosures and we assessed their reproductive development. Using *a priori* models and a curve-fitting approach, we determined the functional relationships between 1) initial and final density; 2) initial density and final mass. We discuss the implications of our results for understanding and modeling amphibian population dynamics.

## METHODS

### *Experimental Pens*

Pens were located in a field at the edge of a wooded area at the University of Missouri's Research Park (Boone County, MO). Each pen was 1 x 2 m, constructed of metal sheeting buried 60 cm into the ground with walls extending 60 cm above ground. We dug a hole 30 cm in diameter and 45 cm deep in the center of each pen, filled the hole with leaf litter and covered it with a 60 x 60 cm plywood coverboard to provide a refuge. We allowed herbaceous vegetation to grow naturally. In addition to the leaf litter under the coverboard, we added approximately 1 kg of dry leaf litter to each pen in the spring and again in late fall. No additional food was added to the pens. All pens were covered with nylon netting (1/4" mesh) that was secured with plastic conduit. This netting provided additional shade typical of closed canopy wood frog habitat and also excluded predators. During periods when no rain fell for more than 10 consecutive days, all pens were watered with the equivalent of 1 cm of rain to reduce the possibility of mortality from desiccation. We watered pens twice for wood frogs and three times for toads.

### *Rearing larvae and stocking pens*

We collected five wood frog clutches from two ponds in Warren County, Missouri on 6 March 2004 and 1,000 American toad larvae from a stream in Boone County Missouri on 12 May 2005. Wood frog eggs were mixed and kept outdoors in wading pools until larvae were free swimming. We reared larvae in 1000-liter cattle tanks filled with water, 1 kg dry leaf litter and 1 liter of phytoplankton and zooplankton inoculum collected from local natural ponds. Wood frog larvae were counted and added haphazardly to tanks on 26 March 2004 and American toads on 12 May 2005. Wood frogs were raised in 20 tanks at a density of 40 larvae per tank and toads in 10 tanks with 100 larvae per tank. We used different larval densities for each species because natural densities for toads are often much higher than for wood frogs, and also because we wanted to use densities that would yield metamorphs comparable in size to those from local natural populations. In natural populations in Missouri, emerging wood frog metamorphs range in size from 14 – 21 mm and toad metamorphs from 12 – 16 mm (unpublished data). We removed metamorphs from cattle tanks when one or both front limbs emerged, and weighed and measured snout-vent length (SVL) for each animal. Wood frog metamorphs weighed 0.34 – 0.98 g (mean 0.67; SD 0.12) and were 15 – 22 mm SVL (mean 20 mm; SD 1.24). American toad metamorphs weighed 0.10 – 0.32 g (mean 0.18 g; SD 0.04) and were 12 – 16 mm SVL (mean 13.6; SD 0.87). Metamorphs were individually marked by toe clipping, with no more than 3 toes clipped per individual.

Wood frog and American toad metamorphs were randomly assigned to the 48 terrestrial pens to ensure that there were no initial size differences among treatments

(wood frog mass: ANOVA,  $F_{390, 5} = 2.24$ ;  $p = 0.98$ ; American toad mass: ANOVA,  $F_{390, 5} = 2.24$ ;  $p = 0.70$ ). Pens were stocked at densities ranging from 1 - 10 animals per  $m^2$ . Estimates of natural terrestrial densities of juvenile wood frogs and American toads are not available in the literature. Annual metamorph production can vary by several orders of magnitude, leading to a broad range of potential natural densities (Berven 1990; Marsh 2001; Semlitsch et al. 1996). Reports of adult wood frog densities range from 0 – 0.75 frogs/ $m^2$  (Heatwole 1961; Regosin et al. 2003; Roberts and Lewin 1979). Given the high ratio of metamorphs to adults in natural populations, (e.g. 20,262 metamorphs to 800 adults (Berven 1990)), terrestrial densities of wood frog metamorphs are expected to be far higher than those of adults. Metamorph densities can be very high near the edges of breeding ponds, e.g. 16 – 52 animals/ $m^2$  for southern toads in South Carolina (Beck and Congdon 1999). We stocked the enclosures with a range of densities that is likely at the high end of those found in natural populations because we wanted to determine the potential for terrestrial density dependence to regulate populations, and therefore chose a range of densities that might be characteristic of populations at or near carrying capacity.

Wood frogs occupied the 48 pens from May 2004 to May 2005 and toads from June 2005 to June 2006. We stocked pens with wood frogs from 20 - 26 May 2004 and with toads the following year from 7 – 10 June 2005. Treatments were randomly assigned to pens within each of two blocks of 24 pens. Density treatments of 2, 3, 4 and 7 animals per  $m^2$  were replicated eight times each; 1 animal per  $m^2$  was replicated 10 times, and 10 animals per  $m^2$ , the highest density was replicated 6 times. The increased number of replicates of the lower densities was done to improve growth and survival estimates for

the treatments in which growth and survival estimates in pens and treatments were necessarily based on fewer animals.

### *Census protocols*

*Wood frogs* - Censuses were carried out at three-week intervals with each census being conducted in a 2 - 4 day period. For wood frogs, we alternated between two types of censuses: 1) a partial census in which three individuals (or two for pens containing only two animals) were haphazardly caught by hand from each pen, identified by individual mark and SVL measured 2) a complete census in which pens were thoroughly searched by hand in an attempt to capture, identify and measure all surviving individuals. The first partial census of wood frog pens was carried out on 15-16 June 2004 and the first full census on 5-6 July 2004. A total of three partial censuses and three full censuses were carried out through the summer and early fall. Wood frogs overwintered in the pens and were censused again 27-30 March 2005, coinciding with the breeding season of the natural populations in Missouri. Wood frogs were removed from pens 12-24 May 2005, with each pen was searched on six different days during this period. Animals were then weighed, SVL measured, and euthanized.

*American toad* - We expected capture probability at each census interval to be lower for toads than for wood frogs because toads are able to burrow, so we increased our search effort by conducting a complete census of all pens at three week intervals rather than alternating between complete and partial censuses. At each census interval, we identified toads by individual mark and measured their SVL. We carried out the first census on 28 June 2005 and the last census before overwintering on 29 Sept 2005. After overwintering

we conducted one census on 15 April 2006 at the time when natural populations began breeding in Missouri. A final census was conducted on 25 May 2006 during which animals were removed from the pens, identified by mark, measured SVL and weighed. We searched the pens an additional five times from 26 – 30 May 2006.

### *Analysis of survival*

All analyses for the two species were run separately because the toad and wood frog experiments were run in separate years with different weather conditions. We used a non-parametric survival analysis to compare survival among the six density treatments for census intervals that occurred before overwintering. Survival analyses were carried out using Minitab 14. Capture probabilities for these intervals were calculated in program MARK (White and Burnham 1999) using a Cormack-Jolly-Seber Model to assess the accuracy of our censuses. However, the survival analyses were run using data adjusted for capture probability in the following way. We assumed that capture probability in the one-year census was 100% because pens were searched multiple times in the final one-year census until no additional animals were found. All individuals captured in subsequent censuses were known to be alive in all previous census intervals they were counted as such and were included in survival estimates. This approach may slightly underestimate the number of survivors in each census interval because it does not account for those animals that were missed in a given census and died before being recaptured in a subsequent census. However, this approach resulted in more reasonable survival estimates for individual pens than Jolly-Seber mark recapture estimates which occasionally yielded population estimates larger than the initial stocking densities.

We estimated the functional relationship between initial stocking density and the density of survivors after one year by fitting five a priori recruitment models to the data using nonlinear regression and ranking the models using Akaike's Information Criterion (AIC, Akaike 1992). We considered the individual pens to be the unit of analysis. Analyses were carried out using DataFit 8.1 (Oakdale Engineering). The five recruitment models included 1) Linear Function  $y = a*x+b$ ; 2) Beverton – Holt  $y = (a*x)/(1+b*x)$  (Beverton and Holt 1957); 3) Ricker function  $y = e^{-x*a}$  (Ricker 1954); 4) Theta-logistic Growth  $y = x-(x^2/a)^0$  (Nelder 1961); and 5) Shepherd function  $y = (a*x)/(1+b*x^c)$  (Shepherd 1982). A positive linear relationship between the initial (x) and final (y) number of individuals per m<sup>2</sup> is indicative of the absence of density dependence. If density dependence is weak, it is described as a decelerating curve by the Shepherd function when  $0 < c < 1$ . Compensatory density dependence is represented by a saturating function described by either the Beverton – Holt equation or the Shepherd function (which simplifies to the Beverton – Holt equation when  $c = 1$ ). A hump-shaped relationship between initial and final density represents overcompensatory density dependence, and can be described by the 1-parameter Ricker function, which is right-skewed, the 2-parameter Theta-logistic growth model, or the 3-parameter Shepherd function when  $c > 1$ . Both the Theta-logistic and Shepherd models are power functions, which allow a range of curve shapes.

### ***Analysis of growth***

We used a repeated measures analysis of variance (ANOVA) to determine differences in growth (SVL) among density treatments over time. Snout-vent lengths

were log transformed to meet the assumption of normality. We analyzed only the data from the equally spaced census intervals prior to overwintering because the repeated measures ANOVA requires equal time intervals. The repeated measures ANOVA does not allow missing values, so we used data only from pens that had at least one capture in each census interval.

For both toads and wood frogs we used a non-linear regression curve-fitting approach to describe the relationship between initial density and log-transformed body mass after one year. We also evaluated the relationship between density after one year and log-transformed body mass after one year to see if the density resulting from mortality over the course of the year was a better predictor of growth than initial density. We used the pen as the unit of analysis, averaging the mass of individuals in pens containing more than one survivor. We compared the fit of three functions to the data 1) linear  $y = a*x + b$ ; 2) exponential  $a*e^{b*x}$ ; and 3) power  $y = a*x^b$ . Models were ranked based on their residual sum of squares.

### ***Assessment of reproductive development***

After removal from the pens, wood frogs were euthanized using Tricaine methane sulfonate (MS222), and were dissected to determine sex and stage of reproductive development. Female reproductive development in wood frogs was determined by the degree of convolution of the oviducts (Fig. 1). Females were categorized as either having: 1) perfectly straight and thin oviducts as are found in metamorphs, 2) oviducts that have begun convolution, but have not yet folded over themselves or widened, 3) convoluted oviducts that fold back over themselves, but have not yet widened, or 4)

convoluted and folded oviducts that have begun to widen. These categories are similar to those described for *Plethodon cinereus* (Sayler 1966). We compared female wood frog reproductive development scores among treatments using a Kruskal-Wallis test. Male reproductive development was assessed by the presence or absence of nuptial pads, which are secondary sexual characteristics that develop in adult males of most frog and toad species during the breeding season (Di Fiore et al. 2005). American toads were not dissected, but were transferred to larger enclosures to determine their response to density release (results reported elsewhere). We compared the proportion of toads in each treatment that reached minimum reproductive size (based on unpublished data from natural ponds in Missouri) by the end of the experiment as an indication of reproductive development.

## RESULTS

### *Survival*

The differences in survival among density treatments from metamorphosis to overwintering were highly significant for both wood frogs (Wilcoxon;  $df = 5$ ;  $\chi^2 = 15.33$ ;  $p = 0.009$ ; Fig. 2a) and toads (Wilcoxon;  $df = 5$ ;  $\chi^2 = 20.42$ ;  $p = 0.001$ ; Fig. 2b). Animals in the highest density treatment experienced the greatest mortality with only 27% survival in wood frogs (compared to 75% in the lowest density treatment) and even lower survival in toads with only 5.8% of individuals surviving to one year in the highest density treatment (Table 1). At the end of one year, average wood frog densities ranged from 0.75 frogs/m<sup>2</sup> in pens initially stocked with 1 frog/ m<sup>2</sup> to 2.7 frogs/m<sup>2</sup> in pens initially containing 10 frogs/m<sup>2</sup>. Average toad densities after one year were generally lower than in wood frogs (0.31 – 0.79 toads/m<sup>2</sup>). However for toads, pens initially stocked with an

intermediate density (4 toads/m<sup>2</sup>) had the highest average density after one year rather than pens stocked at higher densities. For wood frogs, the relationship between initial stocking density and density after one year was best described by the theta logistic growth model and was highly significant (Fig. 3a;  $y = x - (x^2/5.61)^{0.694}$ ;  $F_{46,1} = 57.50$ ,  $p < 0.001$ ) with good predictive power ( $r^2$  adjusted = 0.55). The theta logistic growth model was also the best descriptor of this relationship for the toads; however, the relationship was not quite significant (Fig. 3b;  $y = x - (x^2/2.76)^{0.623}$ ;  $F_{44,1} = 3.51$ ,  $p = 0.067$ ) and had low predictive power ( $r^2$  adjusted = 0.05). Model ranking statistics are shown in Table 2.

For both wood frogs and toads, the period of greatest mortality across treatments occurred in the first 3-weeks after the pens were stocked (Fig. 2). For wood frogs this period was followed by consistent but low rates of mortality in five of the density treatments between the first 3-week census and the last census before overwintering at 18 weeks (Fig. 2a). There was no mortality for wood frogs at all in the lowest density treatment during this period. Toads continued to experience high mortality up to the ninth week after metamorphosis followed by lower mortality between week 9 and overwintering (Fig. 2b). During the overwintering period, wood frog survival was lowest (82%) in the highest density treatment, but high (90 - 97%) within all other treatments. Toads showed a similar overwintering pattern, but with far lower survival in the highest density treatment (32%) and a range of 69 – 92% survival in the five remaining density treatments.

Mean capture probabilities were high for wood frogs (92 – 94% among census intervals prior to overwintering and 89 – 96% among density treatments). Toads were

slightly more difficult to detect, with 76 – 82% probability of capture among census intervals and 71 – 83% among treatments.

### ***Growth***

Growth rates were drastically lower for wood frogs and toads raised at high densities compared to those raised at lower densities (Fig. 4). Differences in growth among density treatments were significant as early as the first three-week census interval and differed significantly among treatments throughout the experiment for both wood frogs (Repeated Measures ANOVA,  $F_{42,5} = 18.68$ ;  $p < 0.0001$ ; Fig. 4a) and toads (Repeated Measures ANOVA,  $F_{12,5} = 3.67$ ;  $p = 0.030$ ; Fig. 4b).

Average mass after one year was nearly 3-fold higher for wood frogs in the lowest density treatment (mean 5.82 g +/- 0.51 S.E.) compared to those raised at the highest density (mean 1.82 g +/- 0.10 S.E.) and twice as great for toads in the lowest density (11.24 g +/- 1.94 S.E.) compared to the highest density treatment (2.95 g +/- 0.66 S.E.). An exponential function best described the relationship between initial density and log-transformed mass of wood frogs after one year and was highly significant with good predictive power ( $y = 0.86e^{-0.15}$ ;  $F_{46,1} = 84.95$ ;  $p < 0.0001$ ;  $r^2 = 0.65$ ; Fig. 4). In toads this relationship was best described by a power function and was significant with moderate predictive power ( $y = 1.70x^{-0.05}$ ;  $F_{25,1} = 10.98$ ;  $p < 0.0028$ ;  $r^2 = 0.31$ ; Fig. 4). Density after one year (i.e. the final density resulting from mortality) was a better predictor of final mass for toads than was initial density ( $r^2 = 0.72$  vs. 0.31), but surprisingly, in wood frogs it was not ( $r^2 = 0.62$  vs. 0.65).

### ***Reproductive Development***

Reproductive development was clearly affected by density for both wood frogs and toads. All female wood frogs in the lowest density treatment (1 frog/m<sup>2</sup>) had oviducts that exhibited some degree of convolution and over 30% had highly convoluted oviducts that were beginning to widen. Only 1 of 16 female wood frogs (6%) that survived in the highest density treatment (10 frogs/m<sup>2</sup>) had any sign of oviduct convolution. The remaining 15 females (94%) in the highest density treatment had perfectly straight oviducts as seen in emerging metamorphs. A total of 86 female wood frogs were dissected with a minimum of 9 individuals from each treatment. Reproductive scores were averaged within pens and the difference among treatments was highly significant (Fig. 5; Kruskal-Wallis;  $H = 25.71$   $df = 5$   $p < 0.0001$ ). Male wood frog reproductive development was also affected by density treatments. Only male wood frogs in the lowest three density treatments (1 - 3 frogs/m<sup>2</sup>) developed nuptial pads within one year (Fig. 6).

A total of 7 toads, all in the lower 3 density treatments, reached minimum reproductive size (50 mm SVL, unpublished data) by the end of the experiment. Eighty percent of surviving toads in the lowest density treatment reached reproductive size, compared to 11% and 10% in the 2 and 3 toad/m<sup>2</sup> treatments respectively (Fig. 7). None of the toads in the highest three density treatments reached minimum reproductive size within a year.

## DISCUSSION

The effects of terrestrial density on the survival, growth and reproductive development of wood frogs and American toads were unambiguous, with low survival, slow growth and minimal evidence of reproductive development in high density treatments. Overall, toads had far lower survival than wood frogs, which could partly be due to differences in weather conditions between years. However, an experiment conducted in the same pens in 2002 - 2003 found similar differences in survival between American toads and another ranid species, *Rana sphenoccephala* (James 2005). The fitted theta logistic growth models describing the relationship between initial density and density of survivors after one year indicate that across the densities included in our experiment, density dependence is compensatory in wood frogs and strongly over-compensatory in toads. These functions suggest a maximum carrying capacity in the pens of 2.62 frogs/m<sup>2</sup> for wood frogs and 1.05 toads/m<sup>2</sup> for American toads. Conditions in the enclosures were favorable, with consistent shade and moisture, and without competition from conspecific adults and other species, suggesting that carrying capacity in the terrestrial environment of natural populations could be much lower than in the enclosures. If that is the case, then density effects would be expected to occur at lower densities, especially in altered and degraded terrestrial habitats.

For both species, the greatest mortality occurred in the first three-week census interval and was primarily density dependent. However, some mortality may have resulted from density-independent factors as well. Mortality resulting from desiccation is likely greatest during the first weeks following metamorphosis because low surface to volume ratio leads to greater water loss in amphibians (Schmid 1965). Rainfall during

the first three weeks of the experiment was relatively high for wood frogs (12.3 cm from 20 May to 15 June 2004; Missouri Historical Agricultural Weather Database, Sanborn Field) and daily maximum temperatures were not extreme (18.3 – 32.3° C). Lower rainfall the following year (4.65 cm from 10 - 28 June 2005) and higher maximum temperatures (26.6 – 33.9° C) could have contributed to increased early mortality among toads. High mortality soon after metamorphosis has also been documented in larger enclosure studies of *Ambystoma maculatum* and *A. opacum* (Rothermel and Semlitsch 2006) and in natural populations of *A. maculatum*, *A. talpoideum*, and *A. californiense* (Semlitsch 1981; Shoop 1974; Trenham et al. 2000).

Overwintering was also a period of high mortality for both species. Survival during this period was much higher among the lower five density treatments, ranging from 84 – 95% among treatments for wood frogs and 69 – 92% for toads. The extremely low survival (32%) of toads in the highest density treatment during overwintering is likely the mechanism driving the observed over-compensatory density dependence. Mortality during the overwintering period likely results from an interaction between density-independent physiological limitations and density-dependent body condition and competition for suitable overwintering refugia. Lack of sufficient energy reserves is the most likely cause of density-dependent mortality during this period. In high density pens, per-capita prey availability is lower and animals may not acquire sufficient lipid and glycogen stores, which are critical to survival during overwintering (Pinder et al. 1992). Lipid stores are necessary to fuel metabolism, and in wood frogs glycogen is converted to glucose which acts as a cryoprotectant (Pinder et al. 1992).

Although mortality reduced the magnitude of the differences in density among the treatments over time, density continued to affect growth throughout the experiment for both wood frogs and toads. Initial density was a good predictor of final mass for both species; however, the relationship had greater predictive power for wood frogs. In toads, final density, (i.e. the density resulting from mortality) was a better predictor of final mass than was initial density. This was not the case for wood frogs, suggesting that although mortality may reduce densities, wood frogs may have a low capacity for compensatory growth, leading to the persistence of the effects of initial density. Growth in amphibians is primarily determined by temperature, water, and prey availability (Jorgensen 1992). Temperature and moisture were consistent across treatments; therefore per capita prey availability is the most likely factor leading to reduced growth in the higher density treatments. Food availability has been demonstrated to affect growth rates and reproductive traits in post-metamorphic amphibians (Scott and Fore 1995).

Differences in growth among density treatments had clear consequences for reproductive development in both species. In natural populations, male wood frogs have been documented to reach maturity in 1 year and females in 1 - 2 years (Berven 1990; Howard 1980). American toads of both sexes can reach reproductive maturity in 1 year (personal observation), with the ability to reproduce in the breeding season one year following metamorphosis. In our pens, only animals in low density treatments reached these reproductive development potentials. None of the animals, male or female, in high density treatments reached reproductive maturity within a year, and the growth rates exhibited in these treatments suggest that reproductive maturity could be delayed for multiple years.

To understand how the effects of density observed in the pens relate to natural populations, it is important to know the range of densities occurring naturally, however, these data are available for very few pond-breeding amphibian species. We are not aware of estimates of natural terrestrial densities of American toads, but some estimates are available for wood frogs. Heatwole (1961) found average densities of wood frogs ranging from 0.13 - 0.75 frogs/m<sup>2</sup> in an upland hardwood swamp in October. The average wood frog densities in our experimental pens by September ranged from 0.85 - 4.8 frogs/m<sup>2</sup> and from 0.75 – 2.7 frogs/m<sup>2</sup> at the end of the study in May. Regosin et al. (2005; 2003) reported average overwintering densities of adult wood frogs ranging from 0 – 0.063 frogs/m<sup>2</sup> in Massachusetts, and Roberts and Lewin (1979) found densities of 0.196 wood frogs/m<sup>2</sup> in Alberta. The difference in these estimates of natural wood frog densities, an order of magnitude, suggests that a wide range of terrestrial densities occurs naturally and that the densities used in our experimental enclosures, while at the higher end of what may be found in nature, are not unreasonable.

Terrestrial densities of juveniles are determined by annual metamorph production, rates of dispersal, survival, and habitat selection. As metamorphs move away from the pond, densities are reduced. Juvenile wood frogs migrate primarily in the first 4 weeks following metamorphosis, after which they settle into summer home ranges, with the majority of individuals settling within 100 m from the pond (Patrick 2007; Patrick et al. 2006). If individuals were distributed evenly within this area, densities might be expected to range from 0 – 0.64 frogs/m<sup>2</sup> in years of high metamorph production (e.g. 20,262 metamorphs as reported in Berven, 1990). However, because both wood frog and American toad metamorphs show strong habitat selection (Patrick 2007; Patrick et al.

2006; Rothermel and Semlitsch 2002; Vasconcelos and Calhoun 2004), individuals are likely clumped rather than evenly distributed, leading to high densities of individuals in high quality terrestrial habitat.

The effects of terrestrial density on survival, growth and reproductive development in both wood frogs and toads in our experiments have strong implications for population regulation in the complex life cycle of amphibians. Reduced survival of terrestrial juveniles has been shown to slow population growth rate far more than similar reductions in aquatic larval survival (Biek et al. 2002). Theoretical models have also shown that for the majority of complex-life history scenarios, recruitment and adult carrying capacity have a far greater effect on population size than does the carrying capacity of the larval habitat (Halpern et al. 2005). Slow growth rates resulting from high terrestrial densities further reduce population growth rate by increasing the age at first reproduction and increasing the probability of mortality before reaching sexual maturity. Wood frogs rarely live beyond 4 years in some populations (Berven 1990), and most breeding female American toads are 4-5 years old (Kalb and Zug 1990), therefore a delay in reproductive maturity substantially increases the probability of mortality before individuals have successfully reproduced and reduces the number of lifetime breeding opportunities. Low juvenile growth rates also mean that individuals are smaller at first reproduction, which results in smaller clutch sizes (Berven 1982), further reducing population growth rate.

Although the traditional view of population regulation in amphibians has centered on single stage regulation at the larval stage, our experimental results together with several published field studies of natural populations (Beebee et al. 1996; Berven 1995;

Gill 1979; Gittins 1983), suggest that terrestrial-stage or multi-stage regulation may be common among pond-breeding amphibians, and should be considered in models of amphibian demography. Recent population models have incorporated aquatic density dependence, but have not included terrestrial density effects (Taylor and Scott 1997; Trenham and Shaffer 2005; Vonesh and De la Cruz 2002). Theoretical models have demonstrated that if density dependence is assumed to occur only in the larval stage when it in fact occurs at multiple stages, the resulting population dynamics (e.g. nonoscillatory, oscillatory, or chaotic) could be fundamentally altered (Hellriegel 2000). The way in which density dependence is incorporated into demographic models can also dramatically affect the accuracy of population viability analyses (Henle et al. 2004). Demographic models, including multistage density effects, are crucial in informing management plans for the conservation of organisms with complex life cycles. Accurate models can be used to 1) assess extinction risk; 2) identify life history stages most likely to respond to management; 3) define the size of reserves necessary to prevent extinction; 4) determine the number of individuals required to establish new populations; 5) set limits on the number of individuals that can be sustainably collected; and 6) determine the number of populations necessary to prevent regional or local extinction (Morris and Doak 2002). However, the accuracy of these predictions depends entirely on the accuracy of the models on which they are based. As areas of suitable terrestrial habitat are reduced and degraded, carrying capacities in the terrestrial environment will likely be reduced, and the effects of terrestrial density may play an even greater role in the dynamics and decline of amphibian populations.

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**Table 1.** Percent survival of wood frogs and American toads from metamorphosis to one year. Juveniles were raised in terrestrial enclosures with initial densities ranging from 1 – 10 animals/m<sup>2</sup>.

Initial Density (animals/m <sup>2</sup> )	N (number of pens)	Survival of metamorphs to one-year ( $\pm$ S.E.)	
		Wood Frogs	American Toads
1	10	75.0% ( $\pm$ 8.33)	25.0% ( $\pm$ 8.33)
2	8	59.4% ( $\pm$ 6.6)	28.1% ( $\pm$ 10.0)
3	8	50.0% ( $\pm$ 5.5)	43.8% ( $\pm$ 12.2)
4	8	54.7% ( $\pm$ 7.4)	19.6% ( $\pm$ 9.8)
7	8	34.8% ( $\pm$ 3.7)	17.3% ( $\pm$ 10.2)
10	6	28.3% ( $\pm$ 4.6)	5.8% ( $\pm$ 2.7)

**Table 2.** Ranking of models describing the functional relationship between initial density and density of survivors after one year for wood frogs and American toads.

Model ranking is based on AIC values.  $K$  is the number of parameters estimated in each model;  $AIC_c$  values are Akaike's Information Criterion adjusted for small sample size;  $\Delta AIC_{ci}$  is the difference between the AIC value for a given model and the AIC value of the best approximating model for each data set;  $w_i$  values are Akaike weights.

Species	Model	K	$AIC_c$	$\Delta AIC_{ci}$	$w_i$
Wood frog	Theta Logistic Growth	2	93.64	0	0.416
	Beverton-Holt	2	93.75	0.11	0.394
	Shepherd	3	95.88	2.24	0.136
	Ricker	1	98.54	4.9	0.036
	Linear	2	99.94	6.3	0.018
American Toad	Theta Logistic Growth	2	134.93	0	0.393
	Beverton-Holt	2	136.60	1.67	0.170
	Shepherd	3	137.06	2.13	0.135
	Ricker	1	136.09	1.16	0.220
	Linear	2	138.08	3.15	0.081

**Figure 1.** Categories of oviduct convolution used to define the degree of reproductive development in female wood frogs. 1) immature 2) beginning to develop 3) convoluted 4) convoluted and widened



1



2

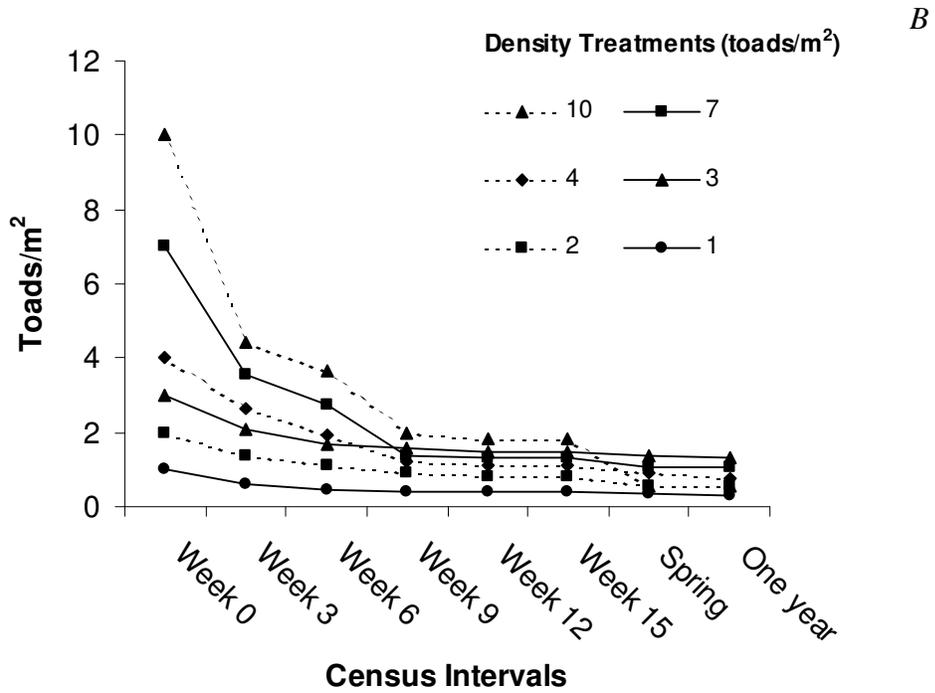
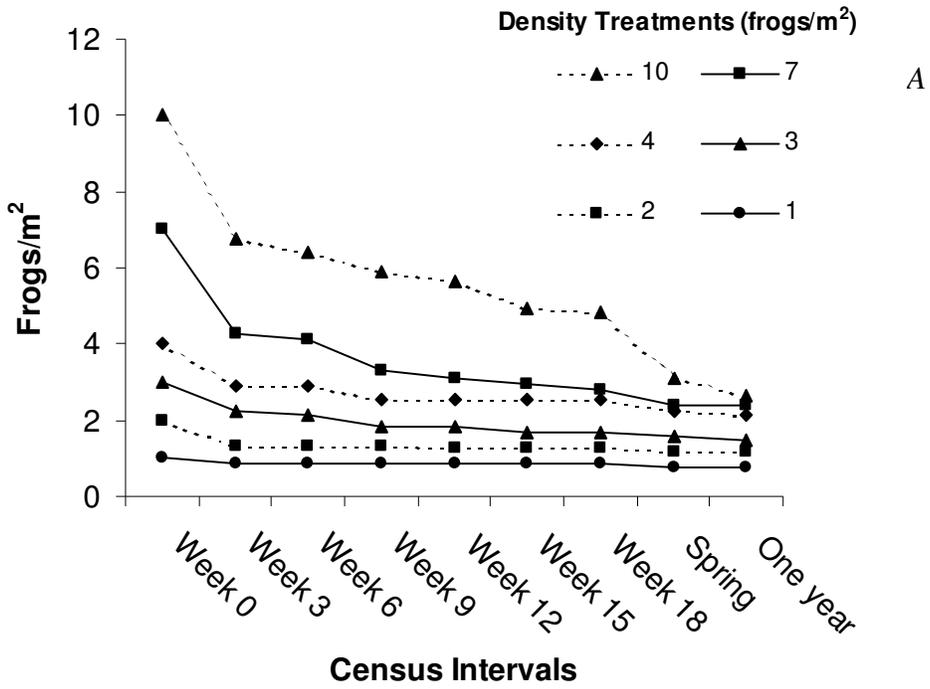


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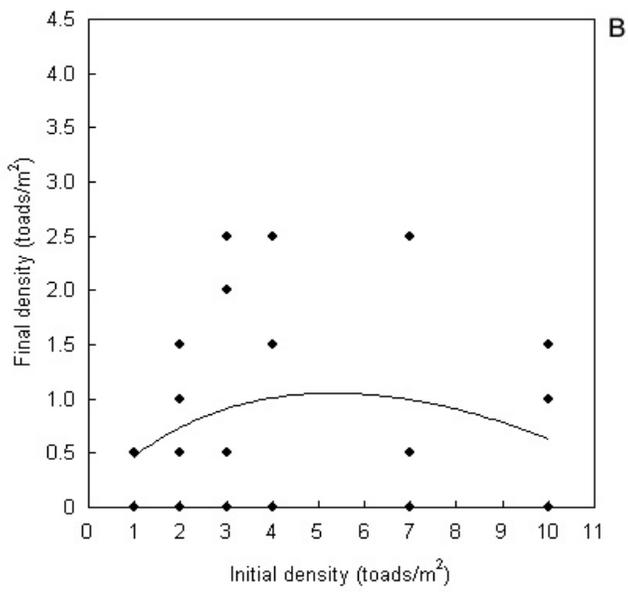
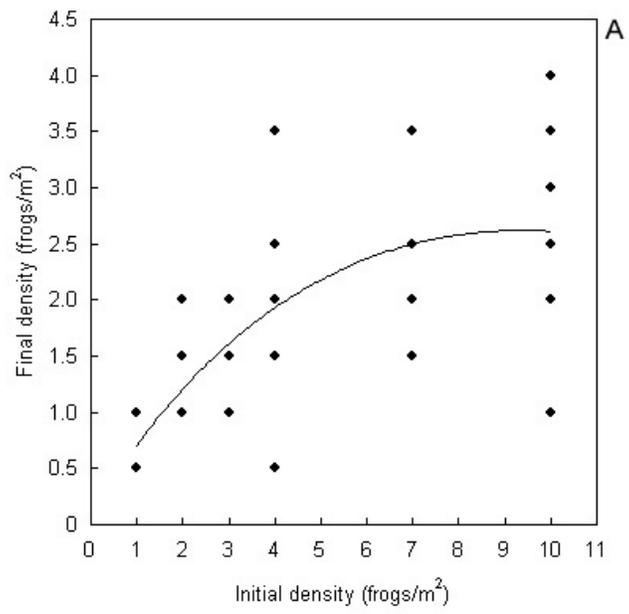


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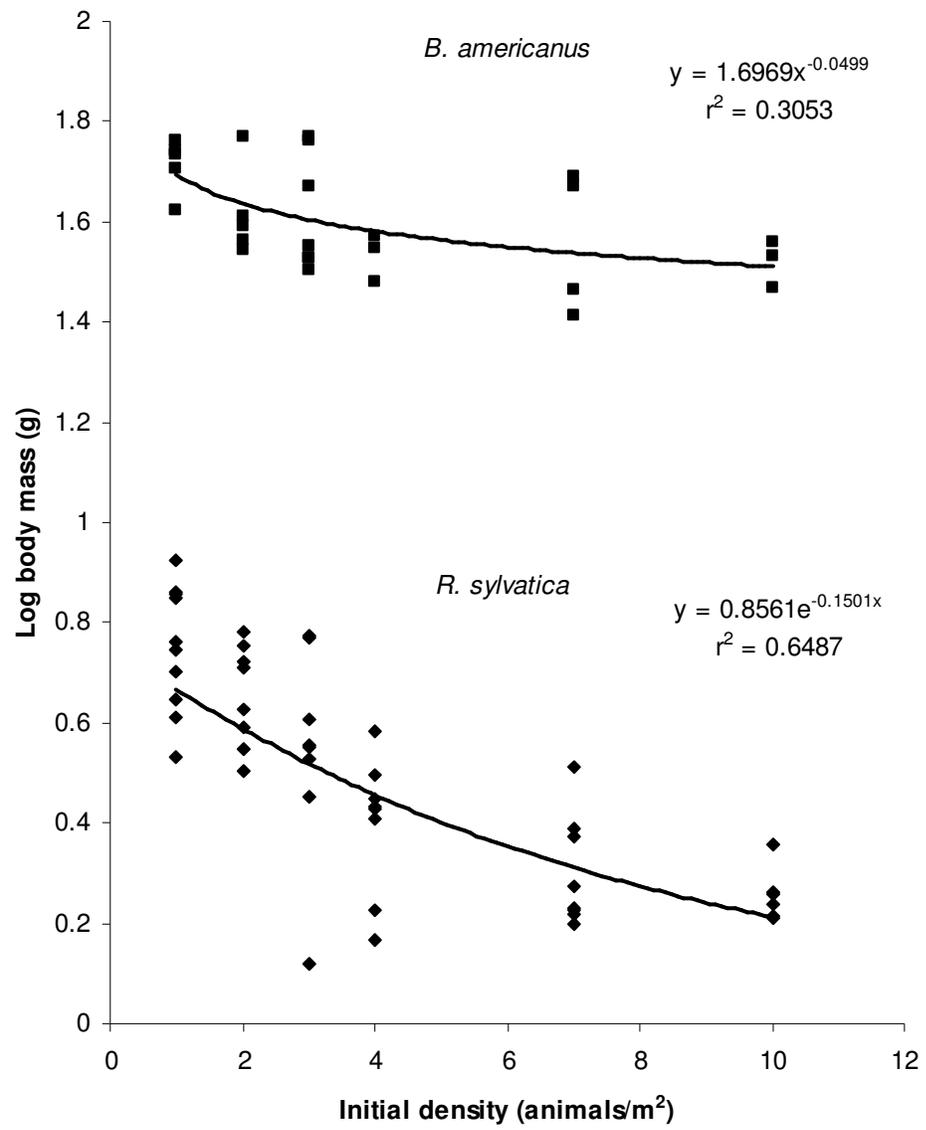
**Figure 2.** Average number of wood frogs (A) and toads (B) (per/m<sup>2</sup>) surviving in terrestrial pens stocked at 6 different initial densities from the initiation of the experiment (week 0) through overwintering until animals were removed from the pens after one year.



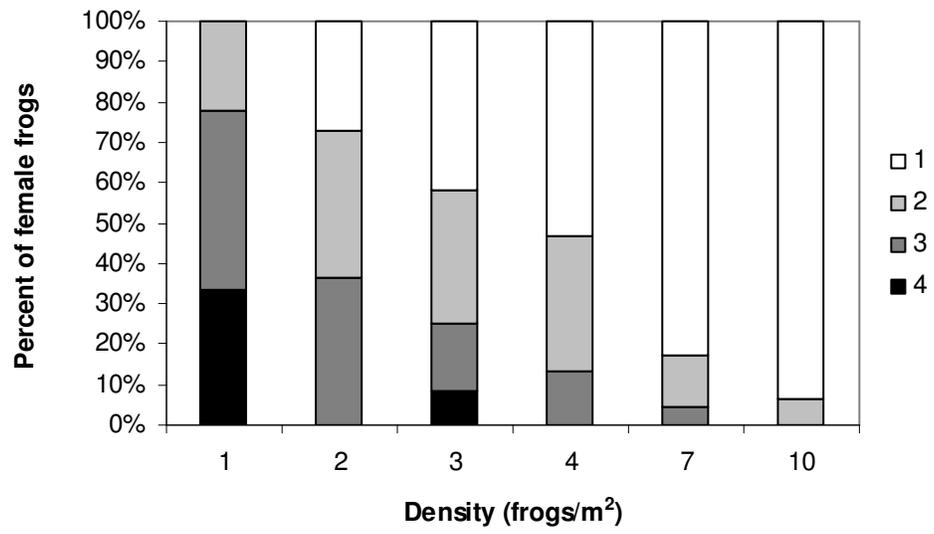
**Figure 3.** Relationship between initial number of animals/m<sup>2</sup> and the number of animals/m<sup>2</sup> surviving to one year for wood frogs (A) and toads (B). Data points represent percent survival in each of 48 1 x 2 m<sup>2</sup> terrestrial pens. The density treatment with 1 animal/m<sup>2</sup> had a sample size of 10 pens; treatments with 2, 3, 4, and 7 animals/m<sup>2</sup> each had sample sizes of 8 pens, and the treatment with 10 animal/m<sup>2</sup> had a sample size of 6 pens. The fitted theta logistic function describing the relationship is shown for both species.



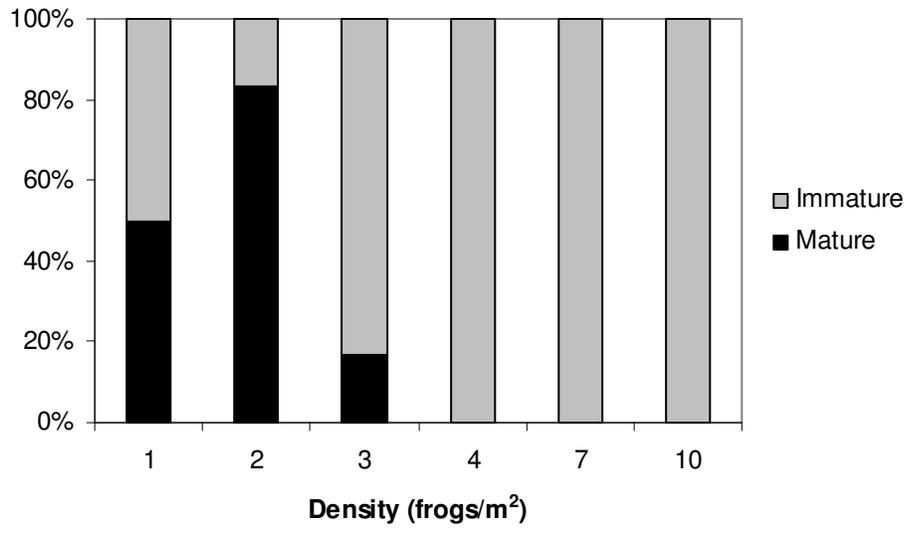
**Figure 4.** Relationship between initial stocking density of terrestrial enclosures and the body mass (log transformed) of wood frogs and toads after one year. Data points represent the average body mass of surviving animals in each of the 48 terrestrial enclosures. Fitted curves are in the form of a power function for the toads and an exponential function for the wood frogs.



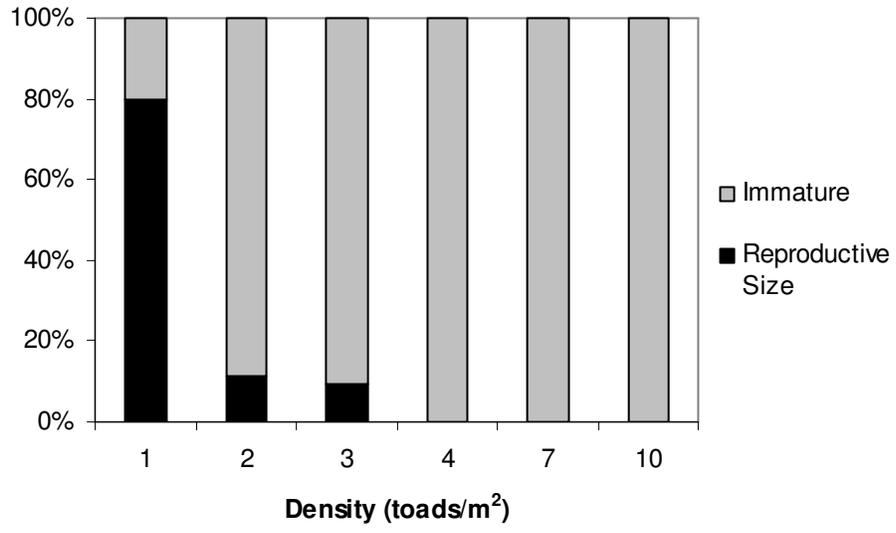
**Figure 5.** Reproductive development of female wood frogs raised at six densities for one year. Colors within each bar represent the percent of wood frogs in each of four categories of oviduct development (1 = immature, 2 = convoluted and narrow, 3 = convoluted and folded over, 4 = highly convoluted and widened). A score of 1 indicates no development while higher scores indicate that individuals may breed in the following season.



**Figure 6.** Percent of male wood frogs raised at 6 densities reaching reproductive maturity within one year. The dark portion of each bar represents the percent of toads exhibiting secondary sexual characteristics (nuptial pads).



**Figure 7.** Reproductive development of American toads raised at six densities for one year. The dark portion of each bar represents the percent of toads that reached minimum reproductive size. The light portion of each bar represents the percent of toads below minimum reproductive size.



## CHAPTER 4

### SURVIVAL OF JUVENILE POND-BREEDING AMPHIBIANS UNDER FOUR FORESTRY PRACTICES IN AN EXPERIMENTALLY MANIPULATED LANDSCAPE

#### ABSTRACT

Many field studies have demonstrated that amphibian abundance and diversity is typically lower in clear-cuts than in uncut forest, however few studies have experimentally manipulated forest habitat to determine the direct effects of forestry practices on amphibian survival. The Land-use Effects on Amphibian Populations (LEAP) project is a landscape scale experimental manipulation designed to determine the effects of three different forestry practices on amphibian populations in three geographic regions of the United States. We report results from studies of juvenile wood frogs (*Rana sylvatica*) and American toads (*Bufo americanus*) raised in 64 terrestrial pens in the LEAP experimental arrays in the Daniel Boone Conservation Area, Warren County Missouri. Over two years, we determined survival rates of 1,584 individually marked juveniles in the first 6 weeks following metamorphosis. We measured habitat and landscape variables within each terrestrial pen and used a regression approach to determine the relationship between survival and these variables. A set of four *a priori* candidate models were developed to explain these relationships, and were ranked using

Akaike's information criterion. We also developed and ranked four post-hoc models. Amphibian survival was highly variable among pens. The best supported models included the variable maximum surface temperature, elevated levels of which can result in direct mortality, but may also function as an accurate composite measure of multiple variables affecting amphibian survival. Our model results indicate that forestry practices interact with existing landscape structure to determine microclimate and thereby influence amphibian survival.

## INTRODUCTION

Forestry practices including clear-cutting have long been associated with reduced amphibian abundance and diversity (e.g. Bennett et al. 1980, Bury 1983, Ash 1988, Petranka et al. 1993, DeMaynadier and Hunter 1996). However, only a handful of studies have experimentally manipulated forest habitat to determine the direct effects of clear cutting on amphibian populations (but see Renken et al. 2004). Whether amphibian abundance is reduced as a result of direct mortality following timber harvest, or because individuals emigrate away from clearcut areas has been a subject of considerable debate (Petranka et al. 1993, Ash and Bruce 1994). Experiments in which amphibians have been confined to clear cut habitat have provided mixed results. Todd and Rothermel (2006) observed high rates of mortality among juvenile *Bufo terrestris* raised in enclosures in clearcuts. In a similar experiment, Chazal and Niewiarowski (1998) found no effect of clearcut habitat on growth, survival or clutch size of mole salamanders, *Ambystoma talpoideum*, raised in four 100m<sup>2</sup> enclosures. In a subsequent study, Rothermel and Luhring (2005) found that burrow availability was a determining factor in the ability of

*A. talpoideum* to survive in clearcuts. In an experiment conducted with 3 anuran species, mortality was high in clearcuts, however rates of survival varied across microhabitats found within clearcuts (Rittenhouse et al.). Rittenhouse et al. also demonstrated differences in survival among 3 species that varied in their behavioral responses to desiccating conditions.

Removal of forest canopy increases the amount of sunlight reaching the forest floor, leading to greater daily temperature extremes and increased evaporative water loss, which in turn results in drier soil and leaf litter (Geiger 1971, Chen et al. 1999). While these conditions can lead to direct mortality, canopy removal also has the potential to exert sub-lethal effects on growth and reproductive development. Increased temperatures and low moisture may lead to decreased prey availability and could also reduce the amount of time that conditions are favorable for foraging. Amphibian responses to these changes may vary depending on geographic region, local forestry practices, rates of forest succession, species specific responses, and many other factors. This variability is just one of many logistical barriers that have contributed to the difficulty in designing experiments aimed at answering the question of how forestry practices affect amphibian populations (discussed in Ash and Pollock 1999).

Our research was conducted within the context of the Land-use Effects on Amphibian Populations (LEAP) project, a landscape scale experimental manipulation designed to determine the effects of different forestry practices on amphibian populations in 3 geographic regions of the United States: Maine, Missouri and South Carolina. In each region, four amphibian breeding sites were chosen and a circular area with a 164 m radius centered on each pond was divided into 4 pie-shaped quadrants, each randomly

assigned one of the 3 forestry treatments, or an unmanipulated control treatment. Within these replicated, landscape scale experimental arrays the project addresses the mechanisms by which forestry practices affect amphibian populations. Comparisons among regions reveal how these mechanisms vary geographically and among focal species.

The LEAP project has focused on pond-breeding amphibians, and more specifically, the terrestrial life history stages of pond-breeding amphibians for which little data are currently available. Many previous studies have focused on the effects of clear-cutting on terrestrial salamanders that have direct development and complete their entire life cycle on the forest floor (e.g. Petranka et al. 1993, Ash 1997, Herbeck and Larsen 1999, Knapp et al. 2003). Less attention has been given to the effects of forestry practices on species that breed in ponds or temporary pools. Although pond-breeding species have an aquatic stage, the majority of their life time is spent foraging and overwintering in the terrestrial habitat surrounding aquatic breeding sites (Semlitsch and Bodie 2003). Recent models of amphibian demography have demonstrated the importance of terrestrial vital rates in determining the growth or decline of populations, emphasizing the need to better understand the effects of land-use practices on the survival of terrestrial life history stages (Biek et al. 2002, Vonesh and De la Cruz 2002).

To determine the effects of the 4 forestry treatments on the growth and survival of recently metamorphosed amphibians, terrestrial enclosures have been constructed at each of the three regional LEAP sites. At the Savannah River LEAP site, Todd and Rothermel (2006) have found low rates of survival of *Bufo terrestris* metamorphs in clearcut enclosures. Here we report results from studies of two anuran species, the American

toad, *Bufo americanus*, and wood frog, *Rana sylvatica*, raised in 64 terrestrial pens in two years at the Missouri LEAP site. American toads are thought to be habitat generalists as adults; however, juveniles may depend on closed-canopy habitat (Rothermel and Semlitsch 2002). Wood frogs are a forest dependent species at the southwestern edge of their range in eastern Missouri and are considered a species of conservation concern within the state. We tracked juvenile survival for both species, measured landscape and habitat variables within the terrestrial pens, and used a logistic regression approach to address two primary objectives: 1) To determine the relative and interacting effects of forestry practices and existing landscape structure on juvenile amphibian survival; 2) To provide predictive models of terrestrial amphibian habitat quality for land managers and policy makers.

## METHODS

### *Study site and experimental arrays*

Our experimental arrays are located in oak-hickory forest of the Central Hardwood Forest Region within the 1,424 ha Daniel Boone Conservation Area (DBCA), Warren County, Missouri, USA (N38°46' W 91°23'). Within the DBCA, approximately 40 fishless ponds originally dug to provide water for game species are currently used by amphibians as breeding sites. From among these ponds we selected 4 sites for our experimental arrays. Each of the 4 arrays consists of 4 pie-shaped quadrants extending 164 m from the central pond. Each quadrant is approximately 2.5 hectares and was randomly assigned 1 of 4 forestry treatments (Fig 1). The distance of 164 m was chosen because it is estimated to contain 95% of the adult population of salamanders that breed

at the central pond (Semlitsch 1998). We centered the arrays only on ponds for which all forest within a 164 m radius was harvested approximately 80 years ago, which is the minimum rotation length used for timber harvest in the DBCA. Because only 3 ponds met this criteria, the 4 forestry treatments in the fourth array were divided between two ponds approximately 300 m from one another, with two forestry treatment quadrants at each pond. The forestry treatments include 1) Control: an unharvested control; 2) Partial Cut: harvesting in which the basal area of the forest was thinned to 60% stocking level by removing or girdling trees considered to be low quality; 3) Clearcut with low coarse woody debris: a cut in which all trees greater than 25 cm in diameter were harvested and removed while trees under 25 cm were girdled and left standing. 4) Clear-cut with high coarse woody debris: a cut as described in the previous treatment, but with trees under 25 cm felled and left within the quadrants, and with debris cut into smaller sections to maximize the amount of coarse woody debris in contact with the ground. Timber harvest was begun February 2004, and application of the treatments was completed by the end of December 2004.

### *Terrestrial pens*

In the fall of 2004, we constructed a total of 64 pens, with 4 pens in each quadrant of the 4 experimental arrays (Fig.1). Each set of 4 pens was located approximately 100 m from the edge of the array's central pond. Pens were constructed of galvanized steel hardware cloth with 0.32 cm mesh to allow small invertebrate prey to move through. Each pen was 3 x 3 m with 30 cm buried below ground and 80 cm above ground with a 10 cm lip around the top. The amount of coarse woody debris (CWD) in each pen was

standardized by treatment, based on data from Shifley and Brookshire (2000). We completely removed CWD from pens in the low CWD quadrants and standardized CWD in pens in the high CWD quadrants. We refer to these treatments within the pens as clearcut with CWD removed and clearcut with CWD retained. We added 2 m of 15 cm diameter CWD of decay class 3 to pens in the control, partial cut and CWD retained pens. Class 3 CWD as defined by Maser et al.(1979) includes logs that are still round, but are faded, lack twigs, and have only a trace of bark remaining. This type of CWD would have been present prior to the application of the forestry treatments. CWD resulting from treatment application is considered decay class 1, which includes round logs with intact twigs and bark (Maser et al. 1979). We added 3 m class 1 CWD to pens in the partial cut and 9 m of class 1 CWD to pens in the CWD retained treatment. In spring 2005, leaf litter depth was standardized by treatment to a depth of 2 cm in the 2 clearcut treatments and 4 cm in the partial cut and control. These depths were based on the averages of measurements taken throughout the forestry treatment quadrants (Rittenhouse et. al. in review). In 2006, leaves were allowed to accumulate naturally in the pens.

### ***Stocking of pens***

We collected toad larvae from ponds at the Daniel Boone Conservation Area in Warren County, MO on 8 June 2005 and 4 May 2006. Wood frog egg masses were collected from the same site on 10 March 2005 and 11 March 2006. Eggs were kept in wading pools before hatching, and larvae were raised to metamorphosis in cattle tanks containing 1000 L water, 1kg leaf litter and 1 L zooplankton and phytoplankton inoculum from local ponds. We stocked cattle tanks at densities of 100 larvae per tank

for American toads and 40 per tank for wood frogs. These densities yield metamorphs that are similar in size to those emerging from natural ponds (E. Harper unpublished data).

Emerging metamorphs were weighed, measured from snout to vent (SVL) and individually marked by toe clipping, with a maximum of 3 toes clipped per animal. Juveniles of both species were stocked at densities of 18 per pen (2 animals/m<sup>2</sup>). In spring 2005 we stocked juvenile wood frogs in 32 pens (2 pens in each quadrant of 4 arrays) and juvenile American toads in 24 pens (2 pens in each quadrant of 3 arrays). These animals were removed from the pens in spring 2006 and 32 pens were then restocked with juvenile American toads or wood frogs, with 1 pen per species in each quadrant of 4 arrays.

### ***Census protocols***

We focused our analysis on survival in the first 6 weeks following metamorphosis, which is the period of greatest mortality during the terrestrial life history stage for many amphibian species (Harper and Semlitsch, Rothermel and Semlitsch 2006). Six weeks following the initial stocking of the pens in both years we searched each enclosure thoroughly by hand in the evening when the animals are most active. Although it is unlikely that we were able to detect 100% of individuals in each enclosure, this sampling technique lead to 71 – 96 % capture probability among sampling periods in a similar study (Chapter 3). To improve estimates of survival at 6-weeks, we conducted an additional search at 12 weeks. Any animals that were captured during this interval,

but undetected in the first census were considered known to be alive at the 6-week interval and were included in our estimate of survival to 6 weeks.

### ***Landscape and microclimate data***

Within each pen we measured the following landscape and microclimate variables: slope, aspect, surface temperature, soil moisture, canopy cover and leaf litter depth. We measured the slope of the ground around each pen using a sighting level (Pocket sighting level, CST/berger, Wateska, Illinois). Aspect was measured using a compass to determine the degrees from North. To track ground surface temperature in each pen we installed temperature loggers in vacuum sealed plastic bags under the leaf litter layer on the soil surface (Thermochron iButton, Dallas Semiconductor, Sunnyvale, California). The iButtons recorded temperatures at 2-hour intervals throughout the study. We also installed soil moisture meters at the center of each pen (Watermark, Irrrometer Co., Riverside, California). Soil moisture measurements (kPA) were taken during periods of drought and following heavy rains to determine the maximum and minimum soil moisture in each pen. We also measured the percent canopy cover over each pen using a convex spherical densiometer and averaging the values of measurements taken at each corner of the pen. Leaf litter depth was measured in each pen in late summer prior to leaf fall in both 2005 and 2006 using a ruler and averaging measurements taken 1 m from each corner of the pen. Measurements of temperature, soil moisture, canopy cover, and leaf litter depth were taken in both 2005 and 2006, while slope and aspect were measured once.

### ***Data analysis***

We compared the values of the microclimate variables among the four forestry treatments using analysis of variance (ANOVA). Four *a priori* models were developed based on hypotheses of the relationships between forestry treatments, microclimate variables and amphibian survival. The Physiological model hypothesizes that amphibian mortality results primarily from temperature and moisture conditions that exceed physiological tolerance. The Forestry Practice model assumes that prior to forest harvest, terrestrial habitat is uniformly suitable; therefore any differences in survival are a direct effect of habitat changes resulting from the forestry treatments. The Landscape model hypothesizes that pre-existing landscape structure determines habitat quality and overrides the effects of timber harvest. The Land Managers' model consists of a subset of parameters that are quick, easy and inexpensive for foresters and land managers to assess in the field and would therefore prove useful as a conservation tool if the model is an accurate predictor of habitat quality. Variables included in these models and our predictions of the relationships between the variables and the number of surviving animals are summarized in Table 1. We used negative binomial regression models ( $\mu = \exp[\text{intercept} + \beta_1 * x_1 + \beta_2 * x_2 + \dots + \beta_n * x_n]$ ) to assess these relationships because many of the pens had no survivors after 6 weeks and the data were not normally distributed. We carried out the analyses using PROC GENMOD in SAS, and ranked models using Akaike's information criterion adjusted for small sample size (AICc). Based on these results we also generated 4 post-hoc models using subsets of the variables included in each of the 4 *a priori* models.

## RESULTS

The application of the four forestry treatments resulted in average canopy cover of 94% in the control pens, 77% in the partial cut, 3% in the clear-cut with CWD retained, and 5% in the clear-cut with CWD removed, resulting in significantly different canopy cover among treatments ( $F_{3,84} = 1650$ ;  $p < 0.0001$ ; Table 2). Leaf litter depth remained similar in both years to the initial standardized depths of 4 cm in the control and partial cut and 2 cm in the two clear-cut treatments ( $F_{3,84} = 5.37$ ;  $p < 0.002$ ; Table 2). The temperature ranges recorded at ground level in the pens were much greater in the two clear-cut treatments than in the control and partial cut treatments, with higher absolute maximum temperatures ( $F_{3,84} = 23.01$ ;  $p < 0.0001$ ) and lower absolute minimum temperatures ( $F_{3,84} = 13.38$ ;  $p < 0.0001$ ) in the clear-cuts (Table 2). Soil moisture was highly variable both spatially and temporally, and our measurements did not detect differences in maximum soil moisture among treatments ( $F_{3,81} = 0.07$ ;  $p = 0.98$ ; Table 2). Minimum soil moisture was also similar among treatments with the exception of the clearcut with CWD retained, which remained wetter than the other treatments ( $F_{3,84} = 2.73$ ;  $p = 0.05$ ; Table 2). The average ground slope of the pens was 16% and ranged from 7 – 34% among pens. Although forestry treatments were assigned randomly, and pens built near the center of each quadrant, there was a significant difference in ground slope among treatments (ANOVA,  $F_{3,60} = 9.16$ ,  $p < 0.001$ ). Pens in the control quadrants tended to be on steeper slopes (mean 22%, range 15 – 28%), while those in the partial cut and clear-cut with CWD retained were both on intermediate slopes averaging 16% (partial: range 8 – 29%, CWD retained: range 9 – 34%). The pens in the clear-cut with CWD removed treatment tended to be on flatter ground, (mean 11%, range 7 – 20%).

Aspect, measured as degrees from north, ranged from 20 – 160° among pens and was not significantly different among the four treatments (ANOVA,  $F_{3,60} = 2.76$ ,  $p = 0.24$ ).

Survival of wood frogs and American toads was highly variable among pens, and no survivors were detected in the majority of pens in either the 6 week or 12 week census interval in both 2005 and 2006. Survival was greater in the second year than in the first, with survivors detected in 40% of pens in 2006 and only 20% of pens in 2005. In pens for which survivors were detected, the number surviving tended to be low, but in one particular partial cut quadrant was consistently very high for wood frogs in both years ( $n = 3$  pens, mean 11, range 10-12). In general, survival was greater among wood frogs than American toads in both 2005 (mean  $\pm$  SE:  $0.69 \pm 0.43$  and  $0.58 \pm 0.21$  survivors/pen respectively) and 2006 ( $2.63 \pm 0.96$  and  $0.63 \pm 0.33$  survivors/pen).

Of the 4 *a priori* models, the Physiological hypothesis best predicted the number of juvenile amphibians surviving to week 6 (Table 4). This model included the variables: species, year, minimum soil moisture, maximum soil moisture, minimum surface temperature and maximum surface temperature, however, maximum surface temperature was the only microclimate variable for which the estimate of beta had a confidence interval that did not overlap zero (Table 7). As predicted, the relationship between survival and maximum surface temperature was negative. Three of the 4 post-hoc models described the data as well or better than the *a priori* physiological model (Table 5). A model including only the variables: species, year and maximum surface temperature ranked highest and predicted decreased survival with increasing maximum surface temperature (Fig. 2). In this model, the confidence interval around the beta estimate for the variable maximum surface temperature did not overlap zero (Table 6).

Two reduced post-hoc versions of the Land Managers' model had a lower AICc values than the *a priori* Physiological model, but still ranked below the post-hoc Maximum Temperature model. In these models, aspect and canopy cover both had beta estimates that did not overlap zero (Table 7). The relationship between survival and aspect (degrees from north) was negative while the relationship between survival and canopy cover was positive (Fig. 3). Correlation coefficients between survival and the variables used in the candidate models are shown in Table 3.

## DISCUSSION

The changes in microclimate resulting from forestry practices that reduce canopy cover had negative consequences for the survival of juvenile wood frogs and American toads in our experiment. However, some landscape variables, such as aspect, were also important, suggesting that both pre-existing landscape structure as well as land-use practices are important determinates of terrestrial habitat quality for amphibians. Of our 4 *a priori* models, the Physiological hypothesis ranked highest, suggesting that the mortality we observed was largely due to microclimate conditions that exceeded physiological tolerance. The best single predictor of survival was maximum ground surface temperature. This variable functions as an accurate composite measure of the effects of both forestry practices and landscape structure, because it is determined by multiple factors including canopy cover, leaf litter depth, understory vegetation, slope, aspect, and microtopography (Saunders et al. 1998). A model including canopy cover and aspect also serves as a composite measure of the effects of forestry practice and

landscape structure on amphibian survival, but ranked slightly below the temperature model in the post-hoc model selection process.

Application of the forestry treatments (partial cut, clearcut with high CWD and clearcut with low CWD) significantly reduced canopy cover, resulting in increased maximum surface temperatures within these treatments relative to the uncut control. Elevated surface temperatures can affect survival directly by exceeding the amphibians' critical thermal maxima, or indirectly by increasing the rate of evaporative water loss and causing dehydration. Short term experiments carried out within the same experimental arrays demonstrated that mortality due to dehydration could occur within 24 hours for both wood frog and American toad juveniles confined to hot, dry microhabitats created by the forestry treatments (Rittenhouse et al.). Reduced leaf litter depth in the clearcuts may also be a factor contributing to increased mortality through desiccation. Leaf litter can significantly reduce the rate of water loss in amphibians (Seebacher and Alford 2002).

Forestry practices may also increase the risk of desiccation by altering soil moisture. Reduced canopy results in decreased interception of rainwater, which can temporarily lead to increased soil moisture relative to unharvested stands, but also results in increased evaporative water loss due to higher surface temperatures. The removal of trees also means that less water is removed through transpiration, so soil moisture is often higher in clearcuts than in forest (Aussenac 2000, Rothermel and Semlitsch 2002). Many characteristics of the landscape, including slope, soil type and hydrology interact with the effects of forestry practices to determine soil moisture, which can be highly variable over space and time. Our measurements of soil moisture were intended to determine the

maximum and minimum soil moisture levels experienced within pens. We found that soil moisture was highly variable even on a small scale (i.e. pens in the same quadrant), but that overall there were not consistent differences among treatments. The only exception to this was in the clearcut with CWD retained pens, in which the soil contained more moisture during the driest period than any of the other treatments. Although soil moisture was a parameter included in our physiological hypothesis model which ranked highest among the *a priori* hypotheses, the beta estimates overlapped zero, indicating that neither maximum nor minimum soil moisture were significant parameters in the model. This does not necessarily indicate that soil moisture is an unimportant factor in determining juvenile amphibian survival, but may indicate that our measurements were not sufficient to characterize the relationship. Our measurements were taken at a single point within each pen and may not have represented the range of soil moisture within the pen from which juveniles were able to choose. Also, our measurements may not have been taken frequently enough to capture the full range of soil moistures experienced within each pen over time. Surface temperature, which was measured every 2 hours, may actually have been a better surrogate measure of soil moisture in our experiment because it represents a composite measure of canopy, litter depth, understory vegetation, microtopography, slope, and aspect, which are all expected to affect soil moisture (Saunders et al. 1998).

Slope and aspect are landscape characteristics that are independent of forestry practices, but can have an important influence on microclimate (Swanson et al. 1988). Our models indicate that forestry treatments interact with landscape variables to determine microclimate and thereby influence amphibian survival. This is an important

concept to consider when making management decisions. More specifically, a particular forestry practice may produce very different effects depending on the topography of a site. In our post-hoc Land Managers' model, which included canopy cover and aspect, we found that aspect was a significant variable in the model. Survival was higher in pens on north-facing slopes than on south-facing slopes where temperatures tend to be higher. Because the average aspect was not significantly different among the 4 forestry treatments, we were able to determine the effect of aspect independent of treatment. Slope, however, was significantly different among treatments and was therefore confounded with treatment, making it difficult to determine the effect of slope on survival. Our study site, the DBCA, is characterized by topography that can be quite steep, with deeply cut drainages and flat ridge tops. When building the pens we avoided drainages where runoff might have caused damage, and also avoided building on very steep slopes. Because of this, the sites where our pens were built do not reflect truly random points and do not reflect the full range of slopes available to frogs within the forest. Radio-tracked adult wood frogs at this site have been shown to move directly to drainages following breeding Rittenhouse and Semlitsch (in review), and these steep-sided ravines may provide cool moist microhabitats that are important to juvenile amphibians at the site as well.

Overall, the survival of juvenile wood frogs and American toads in our study was low, with most pens having no survivors by week 6. This may have resulted in part from the location of the pens, none of which were in drainages, but was likely also due to the unusually hot dry weather at the site in both 2005 and 2006. In 2005, conditions in Warren County ranged from moderate drought in May to extreme drought by August,

with above normal temperatures from June through August (National Climatic Data Center, NOAA). Conditions in 2006 were less severe, however there were still abnormally high temperatures and moderate drought in May and abnormally dry conditions in July. The warmer dryer conditions in both years likely lead to higher mortality than would have been observed in a typical year. In the drought year of 2005, Rittenhouse and Semlitsch (in review) observed 20% mortality of adult wood frogs resulting from desiccation in the DBCA compared to no desiccation mortality in the previous year (2004) in which rainfall was normal. Because of the difficulty in predicting extreme weather events, it may be important when making conservation and land management decisions to consider this worst-case scenario, especially when dealing with species of conservation concern, such as the wood frog in Missouri. Making management decisions based on average weather years could regularly underestimate the effects of canopy removal on amphibian survival whereas estimates based on drought years will yield more conservative estimates.

Survival was lower for American toad juveniles than for wood frogs in both years. This pattern has also been observed in other enclosure studies of these species during non-drought conditions (Harper and Semlitsch). Although adult American toads are considered to be habitat generalists, metamorphs actively select forested habitat (Rothermel and Semlitsch 2002), and are less tolerant of hot dry conditions than are adult toads. Wood frogs, both adults and juveniles, are strongly associated with closed canopy habitat, and juveniles orient towards forest when given an option between forest and clearcut (DeMaynadier and Hunter 1999). In Missouri, wood frogs are at the edge of their range and occupy habitat that is much drier than the sedge-meadows and hummock-

bogs that are typical in the more northern parts of their range (Muths et al. 2005). The extremely variable rates of survival that we observed for juvenile wood frogs may indicate that on the edge of their range, wood frogs are only able to survive in a small subset of the microhabitats that occur within the landscape. Although most pens had no wood frog survivors after 6 weeks, one particular partial cut quadrant had survival of over 50% in both years. It is difficult to determine exactly which characteristics of this area made it suitable habitat for wood frogs, however, it did have a northerly aspect and a maximum surface temperature below the average for both the partial cut and control quadrants.

The spatially patchy survival we observed among American toads and even more dramatically among wood frogs, emphasizes the importance of the interaction of multiple factors including the effects of forestry practices as well as aspects of landscape structure, in determining habitat quality for juvenile amphibians. Our results demonstrate the consequences to juvenile amphibian survival of confinement to habitat patches that ranged greatly in quality. Population growth rates in amphibians are extremely sensitive to reductions in survival of the terrestrial life history stages (Biek et al. 2002, Vonesh and De la Cruz 2002). For populations to remain stable, juveniles must have access to terrestrial habitat that allows survival and growth to reproductive maturity. Our models suggest that conditions exceeding physiological tolerance were the greatest cause of mortality among both wood frogs and American toads. Based on our data, the most effective conservation strategy for amphibians in the DBCA is to identify areas of suitable terrestrial habitat where conditions are cool and moist such as drainages and north-facing slopes, and ensure that forestry practices that reduce canopy cover do not

occur in these areas or cut off access to them. Determining the precise amount of suitable terrestrial habitat necessary to maintain stable populations of amphibians is more difficult however, and will require further work.

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**Table 1.** Parameters included in four *a priori* candidate models describing the relationships between juvenile amphibian survival and landscape and habitat variables. All models include the variables species (wood frog and American toad) and year (2005 and 2006). Predicted  $\beta$  estimates are shown for each parameter.

Model	Parameters	Predicted $\beta$ Estimates
PHYSIOLOGICAL	SPECIES	Wood frog < American Toad
	YEAR	2005 < 2006
	MIN. SOIL MOISTURE (kPa)	< 0
	MAX. SOIL MOISTURE (kPa)	< 0
	MIN. SURFACE TEMP.	< 0
	MAX. SURFACE TEMP.	< 0
FORESTRY PRACTICE	SPECIES	Wood frog < American Toad
	YEAR	2005 < 2006
	FORESTRY TREATMENT	Control > Partial > CWD Ret. > CWD Rem.
	LEAF LITTER DEPTH	> 0
	CANOPY COVER	> 0
LANDSCAPE	SPECIES	Wood frog < American Toad
	YEAR	2005 < 2006
	SLOPE	< 0
	ASPECT ( $^{\circ}$ from North)	< 0
LAND MANAGERS'	SPECIES	Wood frog < American Toad
	YEAR	2005 < 2006
	TREATMENT	Control > Partial > CWD Ret. > CWD Rem
	CANOPY COVER	> 0
	SLOPE	< 0
	ASPECT ( $^{\circ}$ from North)	< 0

**Table 2.** Mean values ( $\pm$  Standard Error) of habitat variables measured within terrestrial pens in each of the four forestry treatments. Means include data from both 2005 and 2006.

Variable	Control	Partial Cut	CWD Retained	CWD Removed
Percent Canopy Cover	94.24 $\pm$ 1.29	77.44 $\pm$ 1.43	3.36 $\pm$ 0.76	5.09 $\pm$ 1.10
Leaf Litter Depth (cm)	2.09 $\pm$ 0.23	2.04 $\pm$ 0.23	1.47 $\pm$ 0.15	1.14 $\pm$ 0.16
Max. Soil Moisture (kPa)	19.95 $\pm$ 1.32	18.27 $\pm$ 1.43	18.20 $\pm$ 0.80	17.41 $\pm$ 1.10
Min. Soil Moisture (kPa)	159.27 $\pm$ 9.46	160.36 $\pm$ 7.81	129.09 $\pm$ 10.09	158.23 $\pm$ 9.11
Max. Substrate Temp. ( $^{\circ}$ C)	33.87 $\pm$ 0.76	38.50 $\pm$ 1.35	47.22 $\pm$ 1.49	46.32 $\pm$ 1.58
Min. Substrate Temp. ( $^{\circ}$ C)	16.14 $\pm$ 0.17	16.55 $\pm$ 0.17	14.36 $\pm$ 0.38	15.34 $\pm$ 0.26

**Table 3.** Correlation coefficients for the number of surviving individuals (N Surv: wood frogs and American toads in both 2005 and 2006) and the variables used in the candidate models.

	N Surv.	Aspect	Slope	Litter	Max. Moist	Min. Moist	canopy	Min. Temp	Max. Temp
N Surv.	1								
Aspect	-0.176	1							
Slope	0.013	0.203	1						
Litter	-0.012	0.012	0.092	1					
Max. Moist.	0.073	0.152	-0.025	-0.210	1				
Min. Moist.	0.039	-0.193	-0.003	-0.003	0.015	1			
Canopy	0.201	0.293	0.431	0.401	0.011	0.159	1		
Min. Temp.	-0.034	0.318	0.182	0.237	-0.146	0.141	0.520	1	
Max. Temp.	-0.278	-0.093	-0.282	-0.338	-0.119	-0.048	-0.671	-0.356	1

**Table 4.** Ranking of *a priori* candidate models based on Akaike’s Information Criterion adjusted for small sample size. Models describe the relationship between amphibian survival and habitat and landscape variables.  $AIC_c$  weight indicates the relative likelihood of each model.

Model	Maximized				
	Log-likelihood	k	$AIC_c$	$\Delta AIC_c$	$AIC_c$ weight
PHYSIOLOGICAL	-2.17	8	22.24	0	0.651
GLOBAL	6.15	15	24.66	2.42	0.194
LAND MANAGERS’	-1.87	10	26.59	4.35	0.074
LANDSCAPE	-6.83	6	26.69	4.45	0.070
FORESTRY PRACTICE	-5.13	9	30.57	8.33	0.010

**Table 4.** Ranking of post-hoc candidate models describing the relationship between amphibian survival and habitat and landscape variables. Ranking is based on Akaike’s Information Criterion adjusted for small sample size, with  $AIC_c$  weight indicating the relative likelihood of each model.

Model	Maximized				
	Log-likelihood	k	$AIC_c$	$\Delta AIC_c$	$AIC_c$ weight
Max. Surface Temperature	-3.89	5	18.53	0	0.711
Canopy Cover and Aspect	-4.16	6	21.36	2.82	0.173
Aspect	-6.09	5	22.91	4.37	0.080
Canopy Cover	-6.88	5	24.53	5.99	0.036

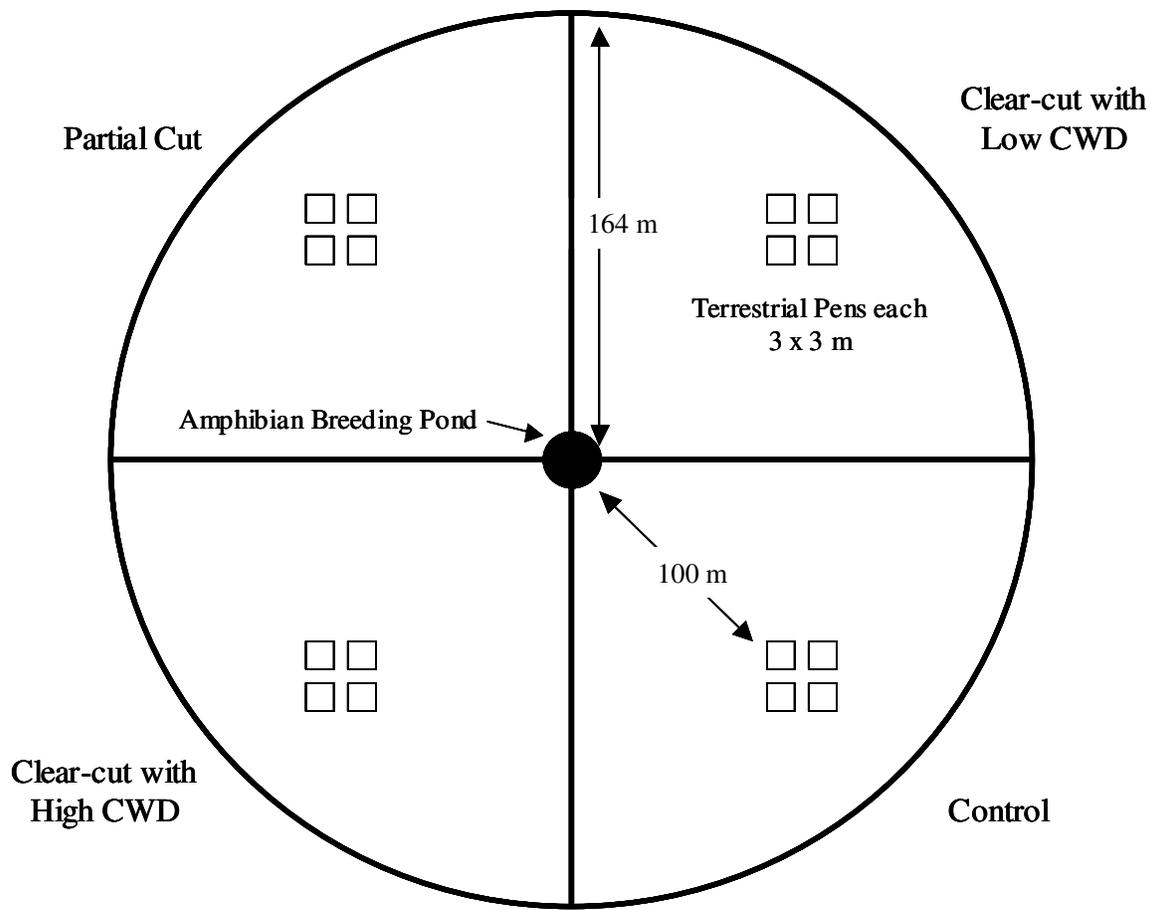
**Table 5.**  $\beta$  estimates and 95% confidence intervals for parameters in the *a priori* model with the greatest support. The Physiological model relates soil moisture and surface temperature to the survival of juvenile wood frogs and American toads.

Model	Point	95% C.I.
Parameter	Estimate	
<b>PHYSIOLOGICAL</b>		
Intercept	15.82	3.63, 28.02
2005	-0.2244	-1.59, 1.14
2006		
American toad	-0.7900	-1.92, 0.34
Wood frog		
Min. soil moisture	0.0014	-0.01, 0.01
Max. soil moisture	0.0092	-0.0280, 0.0463
Min. Surface Temperature	-0.5892	-1.2115, 0.0331
Max. Surface Temperature	-0.1727	-0.2716, -0.0739

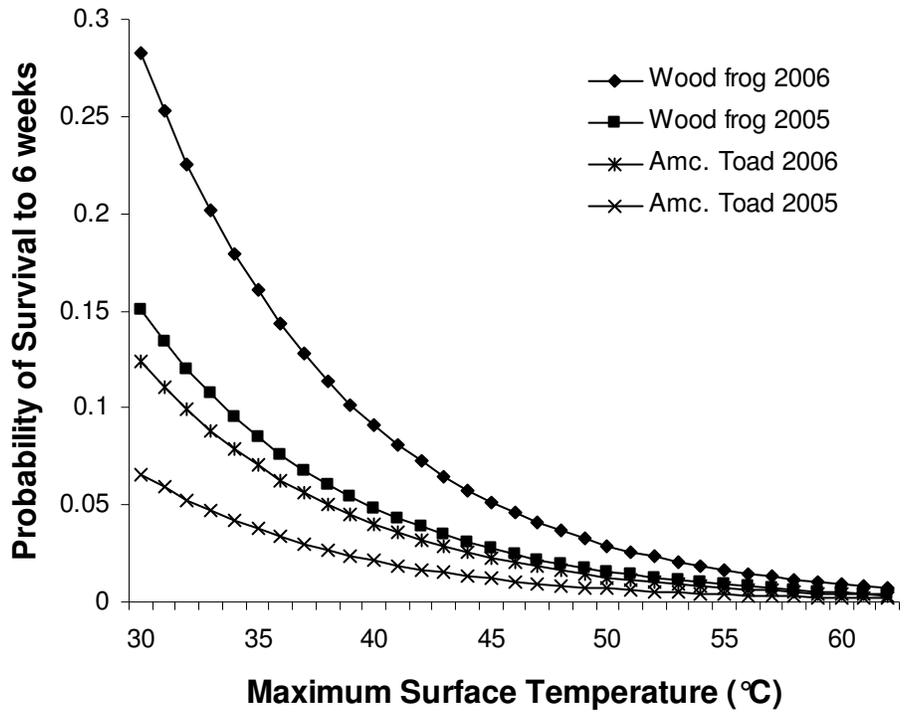
**Table 6.**  $\beta$  estimates and 95% confidence intervals for parameters in two post-hoc models relating habitat and landscape variables to the survival of juvenile wood frogs and American toads. The Maximum Surface Temperature model was the best supported model, however the Aspect and Canopy model also had a lower AIC value than the best supported *a priori* model.

Model	Point	95% C.I.
Parameter	Estimate	
Max. Surface Temperature		
Intercept	5.04	2.15, 7.92
2005	-0.631	-1.62, 0.362
2006		
American toad	-0.825	-1.84, 0.194
Wood frog		
Max. Surface Temperature	-0.114	-0.184, -0.043
Aspect and Canopy		
Intercept	1.06	-0.327, 2.45
2005	-1.07	-2.09, -0.057
2006		
American toad	-0.679	-1.65, 0.295
Wood frog		
Aspect	-0.0116	-0.0211, -0.0021
Canopy	0.0149	0.0028, 0.0269

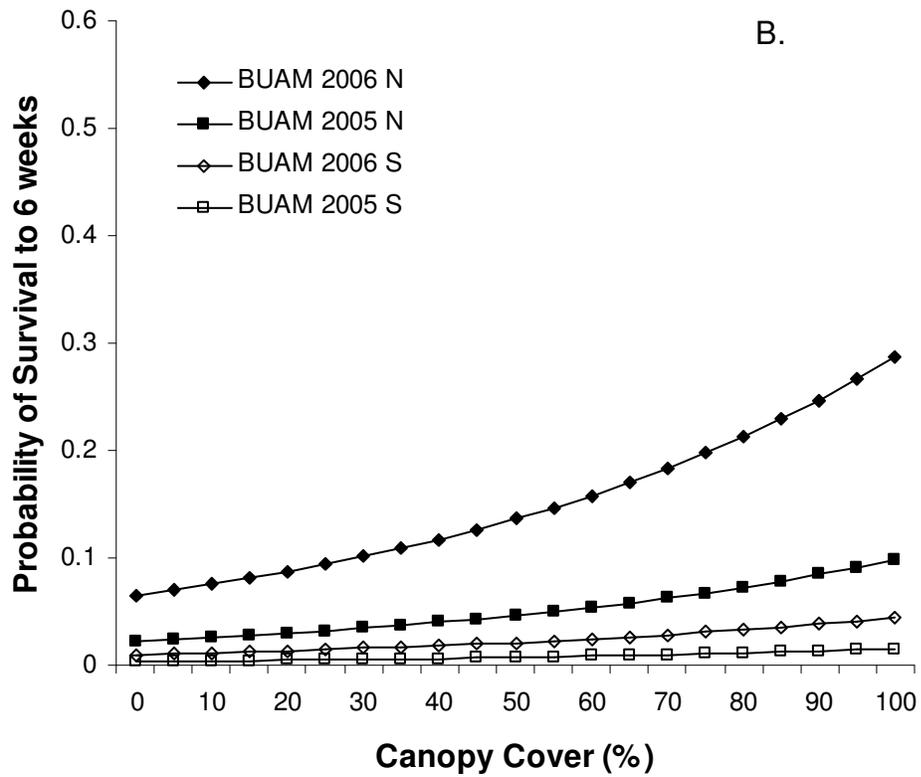
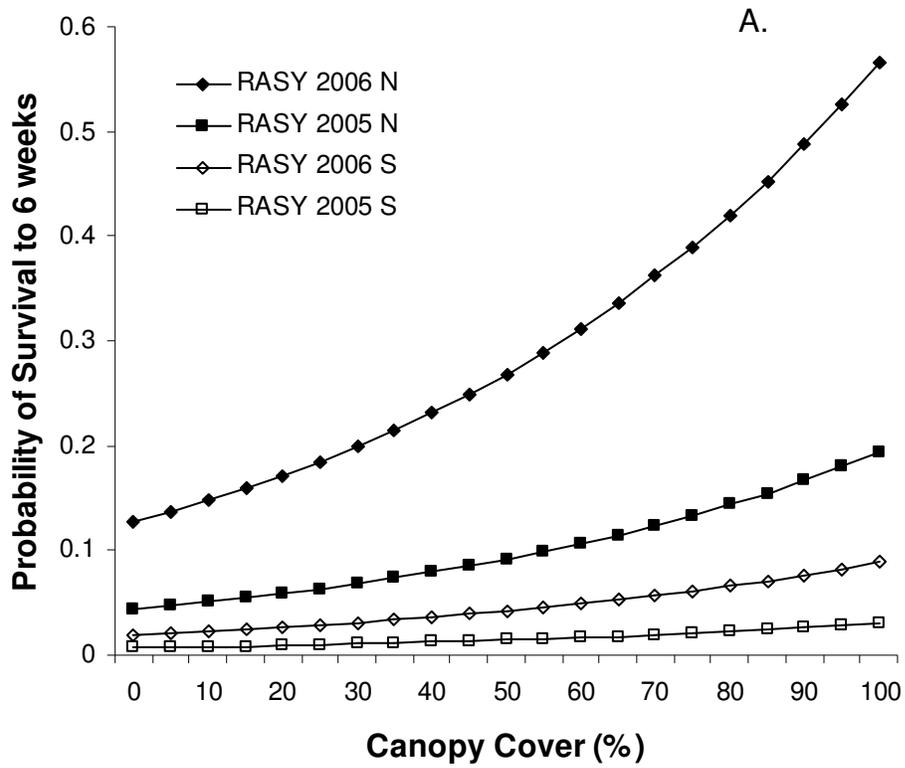
**Figure 1.** Design of experimental forestry arrays used in the Land-use Effects on Amphibian Populations (LEAP) project ( $N_{\text{arrays}} = 4$ ). Terrestrial pens built within these arrays were used to determine juvenile amphibian survival in four forestry treatments: Control, Clear-cut with coarse woody debris (CWD) retained, Partial Cut and Clear-cut with CWD removed. Diagram is not to scale.



**Figure 2.** Survival probabilities for wood frogs and American toads across a range of temperatures. Probabilities are based on the proportion of animals surviving to 6 weeks as predicted by the post-hoc maximum surface temperature model. The temperature range along the x-axis reflects the range of maximum surface temperatures recorded in terrestrial pens in 4 different forestry treatments over 2 years. The model predicts decreasing rates of survival for both species with increases in maximum surface temperature, but with higher overall survival for wood frogs than for American toads. Lower rates of survival in 2005 compared to 2006 are most likely due to differences in temperature and precipitation between years.



**Figure 3.** Predicted survival probabilities for wood frogs (A) and American toads (B) across a range of percent canopy cover on north-facing slopes (solid lines) and south-facing slopes (dashed lines). Probabilities are based on the proportion of animals surviving to 6 weeks as predicted by the post-hoc canopy and aspect model. Survival for both species is greatest on north facing slopes with a high percent canopy cover. Even with a high percentage of canopy cover, predicted survival probabilities are very low on south facing slopes.



## **CHAPTER 5**

### **VIABILITY OF THREATENED WOOD FROG POPULATIONS: QUANTIFYING THE EFFECTS OF REDUCTIONS IN JUVENILE SURVIVAL RESULTING FROM FORESTRY PRACTICES**

#### **ABSTRACT**

Although wood frogs are considered secure throughout most of their range, many disjunct populations at the southern edge of the species' range are threatened. Land-use practices including intensive timber harvesting are thought to be among the primary threats to these populations, however little research has focused specifically on disjunct wood frog populations. To evaluate the population level effects of changes in juvenile wood frog survival resulting from 3 forestry practices commonly used in these regions, we developed a demographic model based on data from wood frog populations on the edge of their range in Missouri. We used the model to 1) evaluate the potential effects of partial cuts, shelterwood cuts and clearcuts on the probability of persistence and size of local wood frog populations; 2) predict the population level effects of reductions in immigration rates associated with forestry practices and 3) test the potential effectiveness of different management options in mitigating the effects of forestry practices. Model simulations demonstrated that changes in juvenile survival resulting from forestry practices can have substantial population level effects, increasing extinction probabilities up to 100% in scenarios in which clear cuts affected all emerging metamorphs and

prevented immigration. However, the magnitude of these effects depended greatly on both the type of forestry practice employed as well as the proportion of emerging metamorphs affected. When all metamorphs in a population were exposed to cuts, and immigration rates were not reduced, partial cuts resulted in extinction probabilities of 8% within a 20 year timeframe; shelterwood cuts resulted in 56% extinction probability; and clearcuts resulted in an 83% probability of extinction. Model outcomes were sensitive to the inclusion of immigration and to the proportion of juveniles in the population that were able to migrate to high-quality habitat in drainages. Our simulations suggest that while some forestry practices could lead to the extirpation of wood frogs populations on the edge of their range, it is possible to carry out small scale cuts while still maintaining wood frog population viability. Management strategies aimed at conserving these populations should recognize the importance of terrestrial habitat and ensure that forested buffers remain around drainages and that connectivity among breeding sites is maintained.

## INTRODUCTION

Many of the amphibian population declines documented in the United States have resulted in severe range contractions, with extinctions of local populations occurring at the edge of species' ranges. Several of these declines have occurred in species that are not considered threatened at a global scale, but may be of conservation concern in specific portions of their range. For example, *Rana pipiens* is ranked 'Least Concern' globally, but has been extirpated from 95% of its former range in California and has experienced severe declines across the western two-thirds of its range (Lannoo 1998). Similarly, many northern populations of *Acris crepitans* have declined to extinction, while at the same time maintaining 'Least Concern' status at a larger scale (Lannoo 1998).

Wood frogs (*Rana sylvatica*) are the most wide ranging amphibian species in North America, with a continuous distribution extending throughout Alaska, Canada, and the northeastern United States (Frost 1985). In the northern portion of its range, wood frogs are considered secure, however, many disjunct populations occurring at the southern and western reaches of the range are threatened (rank S1 - S3, critically imperiled, imperiled or vulnerable, Nature Serve Explorer 2006). As with the majority of threatened amphibians worldwide, habitat loss and fragmentation due to human land-use practices are the primary threats to these populations (Muths et al. 2005). However, very little research has been carried out to evaluate the effects of specific land-use practices on wood frogs at the edge of their range. This lack of data has meant that conservation recommendations for threatened wood frog populations have been based almost

exclusively on data from secure populations that likely have different demographic rates, population dynamics and habitat use than wood frogs at the edge of their range.

Intensive timber harvesting is considered to be one of the primary land-use practices adversely affecting disjunct wood frog populations (Nature Serve Explorer 2006). Many studies have associated forestry practices such as clearcutting with reductions in amphibian abundance and diversity across a wide range of species and geographic regions (reviewed in DeMaynadier and Hunter 1996). However, few studies have experimentally determined the effects of different forestry practices on amphibian survival, making it difficult to assess the population level consequences of specific forestry practices or to evaluate the potential effectiveness of alternate management strategies. The Land-use Effects on Amphibian Populations (LEAP) project is a landscape scale experimental manipulation designed to determine population-level effects of changes in terrestrial amphibian habitat associated with a range of forestry practices. One of the three experimental arrays associated with the project is located in Missouri, where wood frogs are at the edge of their range and are considered vulnerable (Missouri Natural Heritage Program 2007). At this site, survival rates have been determined for metamorph wood frogs raised in terrestrial enclosures under 3 forestry practices and an uncut control forest. Here we assess the population level consequences of these reductions in metamorph wood frog survival and evaluate potential conservation strategies to mitigate these effects.

We developed a stochastic, stage-based matrix population model for the wood frog based on data from the literature and from demographic studies carried out at the Daniel Boone Conservation Area in Warren County, Missouri. We used the models to

perform population viability analyses under a range of management scenarios. Our specific objectives were to: 1) evaluate the potential effects of changes in juvenile survival resulting from 3 forestry practices (partial cut, shelterwood cut and clearcut) on the probability of persistence and size of local wood frog populations; 2) predict the population level effects of reductions in immigration rates that may result from changes in habitat due to forestry practices and 3) test the possible mitigating effects of maintaining forested buffers around drainages, which are known to be important microhabitats for wood frogs at this site.

## **METHODS**

### ***Study Site***

Our model is based on data primarily from populations of wood frogs in the in Daniel Boone Conservation Area (DBCA), Warren County Missouri (N38°46' W 91°23'). The DBCA is owned by the Missouri Department of Conservation and is managed with the goal of providing recreation opportunities as well as the long-term conservation of forests and wildlife. It is a 1,424 ha area of oak-hickory forest in the Ozark Highlands Ecoregion. The topographic relief at the site ranges from 60 – 100 m, and is characterized by flat ridge-tops and steep-sided drainages. Approximately 40 fishless wildlife ponds were constructed on the DBCA between 1960 and 1980 and are currently used as breeding sites by several amphibian species (Hocking et al. in review). The area is sustainably harvested on a 100 year rotation, with cuts averaging 4 – 6 ha. in area. Land managers maintain forested buffers around drainage areas and breeding ponds and do not typically harvest on slopes greater than 35% or on south and west facing

slopes with poor growing conditions (Gus Raeker, personal communication).

Experimental forestry arrays centered around 5 ponds at the DBCA were established in 2004 as part of the LEAP project and include partial cuts, clearcuts with high and low levels of coarse woody debris, and uncut control forest (further details in Harper and Semlitsch further details in Chapter 4).

### ***Model Structure and Parameterization***

We developed a stage-based, stochastic, density-dependent, female-only, post-breeding matrix population model for the wood frog based on data from the literature and from studies carried out in the LEAP forestry arrays in the DBCA. The model consists of stage specific rates of survival and fecundity for each of 3 stage classes: 1) egg to one-year; 2) one-year-old; 3) mature adult (Fig. 1). Because wood frog demographic rates vary geographically (Martof and Humphries 1959, Berven and Gill 1983), we used estimates primarily from populations at the DBCA and when necessary from other populations in the same region. In many cases, however, estimates within this region are available for only a limited number of years, and therefore do not likely capture the true range or mean value of vital rates in these populations. To ensure that our model did not give unreasonable weight to estimates based on single populations or single years, we also included some estimates generated in longer-term studies of wood frog populations in other regions. For parameters that have been shown to vary substantially among years, the model drew values from distributions that included a range of estimates from both DBCA data and other published data, thereby including stochasticity in model simulations. The proportions at which these estimates were drawn were based on a

normal distribution, with intermediate values drawn more frequently than more extreme values. Our goal in developing the model was not to determine current population trends of wood frog populations in the DBCA, but rather to understand the population level consequences of reductions in metamorph survival resulting from forestry practices, therefore, it was preferable to begin with a model of a stable rather than a growing or declining population. To achieve a model with a stochastic log growth rate of 1, we made slight adjustments to the frequency at which values of stochastic parameter estimates were drawn. Further details are provided for each parameter below.

Survival to metamorphosis ( $s_1$ ): Amphibian survival from egg to metamorphosis can vary dramatically among years for most pond-breeding species (Semlitsch et al. 1996). Much of this variation is attributed to differences in temperature and rainfall among years, which affect pre-metamorph survival by determining pond volume and hydroperiod. Increases in pond volume in years with high rainfall can reduce concentrations of predators and competitors, thereby increasing pre-metamorph survival. Conversely, in drought years ponds may dry completely before metamorphs have emerged, resulting in no recruitment (Berven 1990). The majority of ponds in the DBCA never or rarely dry completely, meaning that wood frogs at this site are unlikely to experience ‘catastrophe’ years as a result of ponds drying before metamorphs emerge. However, this absence of pond drying can result in high invertebrate predator densities (Skelly 1995), and high densities of competitors, causing some years with no recruitment. We based our estimates of survival from egg to metamorphosis ( $s_1$ ) partially on data collected from 3 ponds at the DBCA in 2004, a year with normal rainfall and survival

values ranging from 0 – 3%. To simulate environmental stochasticity in pre-metamorph survival,  $s_1$  values were drawn at random from the 3 values from DBCA, the midpoints between these values, and a hypothetical “high rainfall year” with  $s_1$  of 6%. These values were drawn in proportions that result in a mean value of  $s_1$  that is consistent with pre-metamorphic survival rates observed in longer-term studies of wood frog populations (Berven 1990) (Table 1; see also Appendix).

Survival of metamorphs to 6-weeks ( $s_2$ ): We estimated survival from metamorphosis to 6-weeks ( $s_2$ ) separately from juvenile survival to one year because the first few weeks following metamorphosis is a critical period of high mortality for amphibians (Harper and Semlitsch in press, Shoop 1974, Semlitsch 1981, Trenham et al. 2000, Rothermel and Semlitsch 2006). Six-week survival estimates are based on data from metamorph wood frogs raised in terrestrial enclosures in four different forestry treatments in two years at the DBCA (Chapter 4). Results from these experiments indicate that metamorph survival rates are extremely spatially variable and highly dependent on microhabitat conditions, especially ground surface temperature, which is largely determined by percent canopy cover and the aspect (degrees from north) of the microhabitat. We used a predictive model of survival based on canopy cover and aspect reported in Chapter 4 to estimate metamorph survival to 6 weeks under a range of landscape and forestry practice scenarios. This model also includes a year effect that reflects the difference in survival rates between a drought year (2005) and a year with more typical rainfall (2006). To simulate environmental stochasticity in  $s_2$ , model simulations drew randomly from a distribution of possible year effects that considered the drought year effect to result in the

lowest survival rates and the typical rainfall year effect to be the mean. Drought years occurred with a frequency of 10% in simulations.

Juvenile survival from 6 weeks to one-year ( $s_3$ ): Estimates of density dependent survival from 6 weeks to one year ( $s_3$ ) are based on data from a year-long study in which wood frog metamorphs from the DBCA populations were raised in enclosures at a range of terrestrial densities (Harper and Semlitsch). Using these data, we incorporated terrestrial density dependent survival into the model. Because natural densities of juveniles at the DBCA are unknown, we set the minimum value of  $s_3$  to occur whenever the number of juveniles in the population exceeded that resulting from the maximum number of juveniles that could be produced by the largest initial population vector (i.e.  $\max \text{eggs} * \max s_1 * \max s_2$ ). When juvenile numbers were below this value,  $s_3$  was determined by a logarithmic function describing the relationship between the average number of juveniles in the enclosures at 6 weeks and the number surviving to the following spring in (Harper and Semlitsch). Survival from egg to one year is the product of egg survival to metamorphosis ( $s_1$ ), metamorph survival to six weeks ( $s_2$ ) and six-week-old juvenile survival to one-year-old ( $s_3$ ) (Table 1).

Adult survival ( $s_4$  and  $s_5$ ): One-year-old survival to mature adult ( $s_4$ ) and annual adult survival ( $s_5$ ) are equal in our model. The two classes differ only in the proportion that reproduce, with 22% of surviving one-year-olds reproducing the following spring and 100% of surviving mature adults reproducing. Estimates of mean annual adult survival and breeding frequency of one-year-olds are inferred from skeletochronology data from

populations of wood frogs in southern Illinois (Redmer 2002) because estimates of these parameters are not available for populations at the DBCA. Data on survival of radio-tracked adult wood frogs at DBCA in both a drought year and a year with normal rainfall suggest a 20% reduction in survival due to drought conditions (Rittenhouse and Semlitsch, in review). To incorporate this environmental stochasticity, adult survival rates were drawn from three possible values including a mean value inferred from Redmer (2002) and values that are  $\pm 20\%$ . These were drawn at random with the frequency of the average value 4 times that of either the drought year value or the high survival value (Table 1).

Fecundity ( $f_1$  and  $f_2$ ): We used measurements of body length of breeding adult wood frogs from 5 ponds at DBCA ( $n_{\text{frogs}} = 48$ ) and a function from (Berven 1988) that relates female wood frog body size to clutch size to determine the mean and range of clutch sizes used in our simulations (Table 1). Density dependent fecundity has been observed in populations of wood frogs in Michigan, Maryland and Virginia (Berven 1995). In our simulations, clutch size was dependent on the total number of one-year-olds and adults in the population and was defined by a linear relationship in which the minimum clutch size occurred when the population was at carrying capacity and the maximum clutch size occurred when the population consisted of only one adult. Carrying capacity in the model is defined as a total of 97 one-year-olds and mature adults and is based on egg mass surveys of 33 ponds at DBCA in which one outlier population consisted of 97 egg masses, nearly 3 times the number of egg masses as the next largest population in the sample (Rittenhouse unpublished data). Fecundity of one-year-olds ( $f_1$ ) is the product of

clutch size, 0.50, which assumes half of the eggs are female, one-year-old survival (because the model is post-breeding and individuals must survive to the end of the year to breed), and the probability of reaching maturity and breeding before the end of the second year. Adult fecundity ( $f_2$ ) is the product of clutch size, 0.50, and adult survival. All mature adults are assumed to breed every year.

### ***Model Projections***

Model simulations were run using Matlab version 7.0.1. We projected wood frog populations forward 20 years for 30 runs of 5,000 simulations to determine extinction probabilities and mean and median population sizes under a range of landscape and forestry practice scenarios. Populations were considered extinct when the number of one-year-olds and adults was less than one. Initial population sizes for each simulation were drawn randomly in equal proportions from 6 possible initial population sizes. These population sizes were based on egg mass surveys of 33 breeding sites at DBCA (Rittenhouse unpublished data) and ranged from 7 – 47 total adults and one-year-olds. We used the carrying capacity estimate of a total of 97 adults and one-year-olds to place a cap on population size. We included immigration in the model by adding 5 one-year-olds to the population in random years at a frequency of one successful immigration event every 4 years (annual probability of 0.25).

The landscape and forestry scenarios included in our simulations were designed to predict the effects of 3 different forestry practices (thinning, shelterwood cut, and clearcut) on wood frog populations in the DBCA. In model simulations, the effect of each forestry practice is expressed as a change in survival of metamorphs to six weeks

(s<sub>2</sub>) as defined by the canopy and aspect model reported in Chapter 4. Thinning is defined as canopy cover of 77%, a shelterwood cut maintains 30% canopy and a clearcut is defined as 4% canopy cover. These estimates of canopy cover are based on data from experimental cuts in the DBCA (see Chapter 4) and from personal communication with DBCA land managers. Because aspect, as well as canopy cover, affects metamorph survival to six weeks, it was necessary to define the aspect of the habitat in model simulations. Metamorph survival on north facing slopes in DBCA is five times greater than survival on south facing slopes (Chapter 4). Because metamorph wood frogs have been shown to avoid poor quality habitat (Patrick et al. in review), we assume in our models that they avoid habitat on south-facing slopes and migrate primarily into north-facing habitat (50% of individuals) with some individuals (25%) dispersing to east and west-facing habitat patches. These proportions were held constant in all model simulations.

Studies of dehydration rates of juvenile wood frogs in different microhabitats found within forests and clearcuts at the DBCA suggest that habitat in forested drainages is of higher quality than that on forested ridgetops, with short-term survival rates over twice as high (Rittenhouse et al. in review). Radio-tracked adult wood frogs at DBCA have also been shown to migrate to drainage habitat following breeding (Rittenhouse and Semlitsch in review), further suggesting that microhabitats found within drainages are important to wood frogs at this site. Because we do not have data on six-week survival rates of wood frog metamorphs in drainage habitat, we assumed in our models that the highest possible survival in these areas (i.e. survival when the year effect represents a high precipitation year) is equal to the highest observed six-week survival rate (85%)

reported for wood frog metamorphs raised in terrestrial enclosures that were watered regularly to minimize desiccation risk Harper and Semlitsch (in press). This resulted in estimated survival rates in forest drainages approximately 10% higher than those estimated for non-drainage forest habitat (range 24 – 85% depending on year effect).

In model simulations we varied 3 factors: 1) percent canopy cover (94% in uncut forest, 77% in partial cuts, 30% in shelterwood cuts, and 4% in clearcuts); 2) The relative proportions of metamorphs migrating to forested drainage habitat, uncut forest other than drainages, and cut forest; 3) Whether or not there was successful immigration into the population. The population growth rate is stable when 50% of emerging metamorphs migrate to drainage habitat, 50% migrate to uncut forest, and successful immigration occurs with an annual probability of 25%. Varying these factors allowed us to estimate the population level effects of forestry practices that reduce canopy cover and may change the amount of available forested drainage habitat and the degree of connectivity among local populations.

## **RESULTS**

Our model simulations showed strong population level effects of changes in metamorph survival resulting from forestry practices that reduce forest canopy cover. Model results were also sensitive to changes in immigration rates and to the availability of high-quality drainage habitat. As the proportion of emerging metamorphs in the population that migrated into harvested forest increased, the probability of local extinction increased and median population sizes decreased (Figs. 2 and 3). In partial cuts, which maintain 77% canopy cover, extinction probabilities increased from less than 1% to a 7.7% probability of extinction within 20 years as the percentage of affected

metamorphs increased from 0 – 100% (Fig. 2A). In partial cut simulations, a 95% probability of persistence could be maintained as long as no more than 80% of metamorphs were affected by the cut, and immigration rates were not reduced. The effects of shelterwood cuts on extinction probabilities were far greater than those of partial cuts. Extinction probabilities were as high as 56% when all metamorphs were exposed to shelterwood cuts, even when immigration rates were not reduced (Fig. 2B). Only shelterwood cuts affecting less than 40% of metamorphs maintained a greater than 95% probability of persistence over 20 years. Clearcuts resulted in extremely high extinction probabilities, with 83% of local populations reaching extinction within 20 years when all metamorphs were affected (Fig. 2C). However, the 95% probability of persistence threshold was the same in both clearcuts and shelterwood cut simulations, requiring that fewer than 40% of metamorphs are affected.

Median population sizes were substantially reduced by decreases in metamorph survival associated with canopy removal, even in model simulations that maintained a greater than 95% probability of persistence over 20 years. For example, in simulations in which 80% of metamorphs were affected by partial cuts, median population size was reduced by half (Fig. 3). Likewise, simulations with 40% of metamorphs affected by shelterwood cuts or clearcuts resulted in reductions of median population sizes of one third and one half respectively (Fig. 3).

Model simulations were highly sensitive to the proportion of metamorphs that were able to migrate to high-quality drainage habitat. The effects of canopy removal were substantially reduced when the proportion of metamorphs migrating to drainages was held constant at 50%. Even simulations in which the remaining 50% of metamorphs

were exposed to clearcuts, extinction probabilities were less than 95% over 20 years (Fig. 4). With half of metamorphs in drainages and half in forestry treatments, median population sizes were reduced from 27 to 24 in partial cuts, 18 in shelterwood cuts and 15 in clearcuts (Fig. 5). Even in the absence of forest canopy removal, reductions in the percentage of metamorphs in the population (from 50% to 0) migrating to drainage habitat rather than uncut forest had a substantial effect on population size and extinction probability, with a 32% reduction in median population size and a three-fold increase in extinction probability within 20 years.

Model predictions were also sensitive to changes in immigration rates, with the absence of immigration resulting in substantially higher extinction probabilities (Fig. 6). Simulations without successful immigration and in which all metamorphs were exposed to a forestry treatment resulted in 20-year extinction probabilities of 30% in partial cuts, 97% in shelterwood cuts and 99.9% in clearcuts. To maintain a 95% probability of persistence over 20 years in the absence of immigration required that less than 10% of metamorphs were affected by any of the three forestry treatments. Without successful immigration, populations in which all metamorphs were exposed to shelterwood cuts or clearcuts reached below the 95% probability of persistence threshold within 4 years (Fig. 6 B and C). The absence of immigration also resulted in substantially smaller median population sizes (Fig. 7).

## **DISCUSSION**

Our model simulations demonstrate that forestry practices leading to reductions in survival of wood frogs in the first six weeks following metamorphosis can have

substantial population level consequences, including declines in population size and increased extinction probabilities of up to 100%. However, the magnitude of these effects depends greatly on both the type of forestry practice employed as well as the proportion of emerging metamorphs affected by the reduction in canopy cover. Based on our simulations, the maintenance of wood frog populations with greater than a 95% probability of persistence over a 20 year time frame requires that fewer than 40% of emerging metamorphs are affected by either shelterwood cuts or clearcuts, while up to 80% of metamorphs can be affected by partial cuts while still maintaining a 95% probability of persistence. While large-scale cuts are likely to affect 100% of metamorphs in a population, thereby reducing population viability below 95% with the use of any of the 3 forestry practices, the smaller scale cuts (4 – 6 ha.) typical of conservation areas in Missouri may affect only a proportion of emerging metamorphs.

Unfortunately, the spatial distribution of metamorph wood frogs in the terrestrial environment at this site is unknown, making it difficult to determine the proportion of metamorphs likely affected by cuts of specific sizes and spatial arrangements. Studies of juvenile wood frogs in Maine have shown that individuals actively select high quality habitat, leading to an uneven distribution of juveniles in the terrestrial landscape (Patrick et al. in review). Because terrestrial habitat quality is extremely patchy for wood frogs at the DBCA, even within specific forestry treatments (Harper and Semlitsch, Rittenhouse et al.), it is expected that metamorphs have a correspondingly clumped distribution in the landscape. Further research is necessary to determine how behaviors of emerging metamorphs, including habitat selection and movement rates, affect the distribution of juvenile wood frogs in the terrestrial habitat. Until these data are available, land

managers can likely conserve wood frog populations without completely eliminating the use of small scale clearcuts and shelterwood cuts, by identifying the microhabitats that result in high metamorph survival, and reducing the degree to which these microhabitats are affected by forestry practices.

Microhabitats found within forested drainages have been shown to result in higher wood frog metamorph survival than those found on forested ridgetops in the DBCA (Rittenhouse et al.). Although the use of these microhabitats by juvenile wood frogs has not been confirmed, radio-tracked adult wood frogs at this site preferentially select drainage habitat following breeding migrations (Rittenhouse and Semlitsch in review). Our models demonstrate that the increased survival rates in these microhabitats could substantially improve the viability of populations exposed to forestry practices if 50% of emerging metamorphs have access to and select forested drainage habitat. In these simulations, even when the remaining 50% of metamorphs were exposed to clearcut habitat, populations still maintained a 95% or greater probability of persistence. Maintaining forested buffers around drainage habitat and connecting these buffers with forested buffers around breeding sites would likely increase the proportion of emerging metamorphs that are able to migrate to high quality habitat.

The maintenance of undisturbed corridors between breeding sites could also improve population viability by increasing immigration rates. In our model simulations, forestry practices that cut off immigration from neighboring populations led to extinction probabilities approaching 100% within 20 years if all metamorphs were affected by either shelterwood cuts or clearcuts. Natural rates of immigration in undisturbed landscapes are largely unknown for most amphibian species and are likely to be highly variable,

depending to a large degree on factors including distance between breeding sites, density of breeding sites in the landscape, quality of terrestrial habitat between neighboring ponds, environmental stochasticity, and fluctuations in numbers of metamorphs produced in neighboring breeding sites. Genetic studies of wood frogs provide evidence for significant gene flow among populations even when separated by distances of more than 1 km (Squire and Newman 2002). A study by Berven and Grudzien (1990) found that approximately 18% of metamorphs in four wood frog cohorts in Virginia bred in ponds other than their natal pond, however the number and frequency of successful immigration events at the ponds to which the frogs emigrated were not reported. The immigration rates included in our simulations (immigration of 5 one-year-olds with an annual probability of 25%) may be higher or lower in specific populations depending on any of these factors. However, the sensitivity of the model predictions to the elimination of immigration suggests that while we may not have precise estimates of immigration rates, it is reasonable to conclude that immigration is important to wood frog population viability. This is not surprising considering that wood frogs are relatively short-lived and are vulnerable to frequent catastrophe years with no recruitment (Berven 1990), making local extinctions highly likely in the absence of immigration. Conservation measures aimed at increasing immigration rates should include the maintenance of high quality terrestrial habitat between existing ponds. Immigration could also be improved by increasing in the number of breeding sites with intermediate hydroperiods, thereby decreasing the distance between breeding sites and maximizing the number of metamorphs produced (Pechmann et al. 1989).

Our model simulations suggest that it is possible for land managers to balance land-use practices and the maintenance of viable wood frog populations. Efforts to conserve disjunct wood frog populations at the edge of their range in Missouri must consider aspects of terrestrial habitat quality if they are to be successful. Forestry practices affecting all metamorphs in a population simultaneously and reducing juvenile survival and immigration can result in extremely high rates of local population extinction. However, population viability can likely be achieved with small-scale cuts that maintain forested buffers around breeding habitat and high quality drainage habitat, and that facilitate juvenile immigration. Conservation recommendations could be strengthened by additional research focusing on the distribution of juveniles in the terrestrial habitat, natural rates of immigration, and the effects of forestry practices on adult wood frogs.

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**Table 1.** Parameter estimates used in stochastic simulations of wood frog population dynamics.

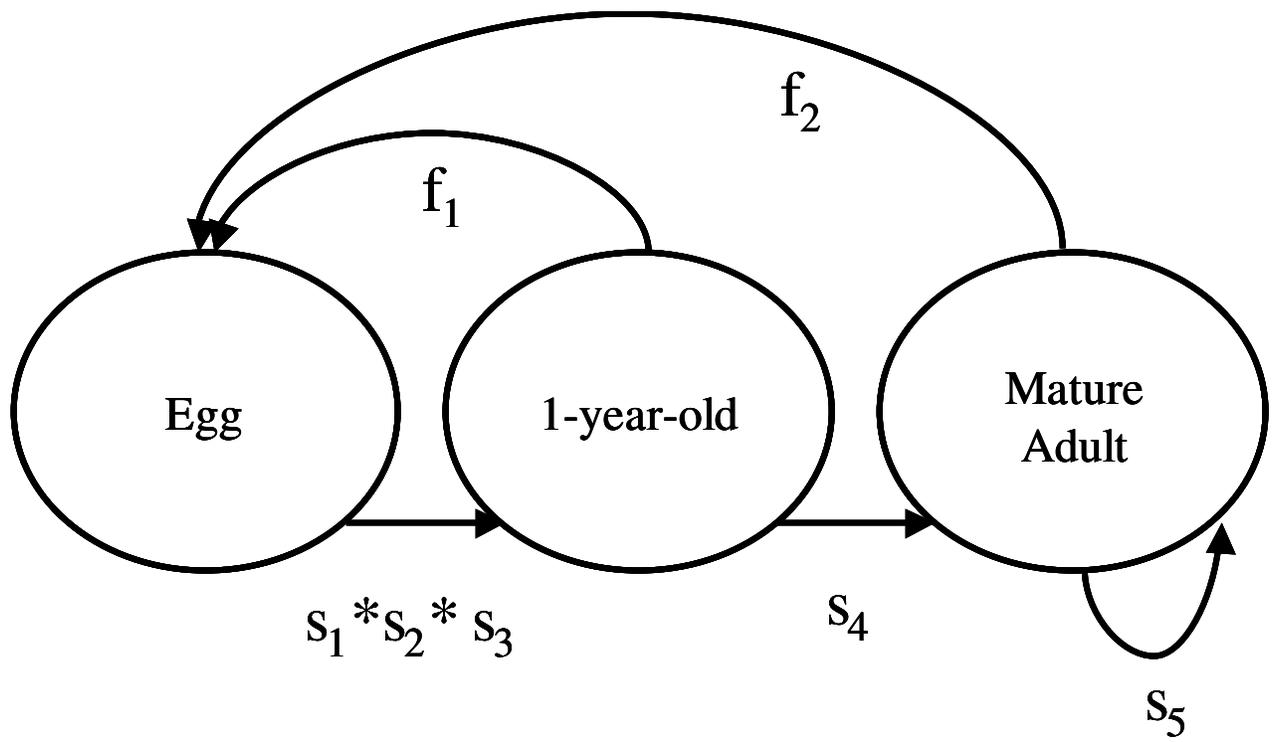
<b>Parameter</b>	<b>Min.</b>	<b>Max.</b>	<b>Mean <math>\pm</math> Std. Dev.</b>
Egg survival to metamorphosis ( $s_1$ )	0	0.060	0.0193 $\pm$ 0.0165
Metamorph survival to 6 weeks ( $s_2$ )	0.200	0.690	0.4224 $\pm$ 0.1271
6-week-old survival to 1-year ( $s_3$ )*	0.480	0.900	0.8951 $\pm$ 0.0060
Egg survival to one-year ( $s_1*s_2*s_3$ )*	0	0.037	0.0071 $\pm$ 0.0066
1-year-old survival to adult ( $s_4$ )	0.34	0.52	0.4117 $\pm$ 0.0151
Annual adult survival ( $s_5$ )**	0.34	0.52	0.4117 $\pm$ 0.0151
Clutch size*	643	987	904 $\pm$ 24.18
Probability of 1-year-old breeding (the following spring)	0.22	0.22	0.22
Fecundity of 1-year-olds ( $f_1$ )*	24	56	41.11 $\pm$ 2.318
Fecundity of adults ( $f_2$ )*	109	257	186.9 $\pm$ 10.54

\* Parameter is density dependent in model simulations. Means and Std. Dev. are based on simulations that assume all emerging metamorphs migrate to habitat with continuous canopy cover.

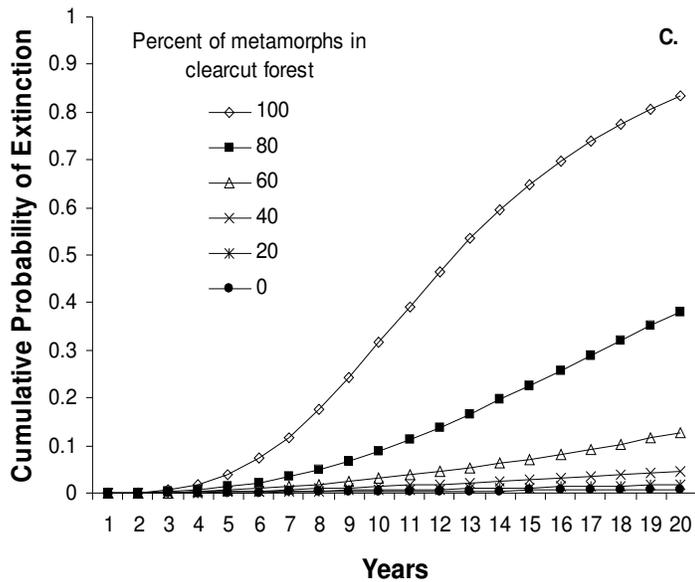
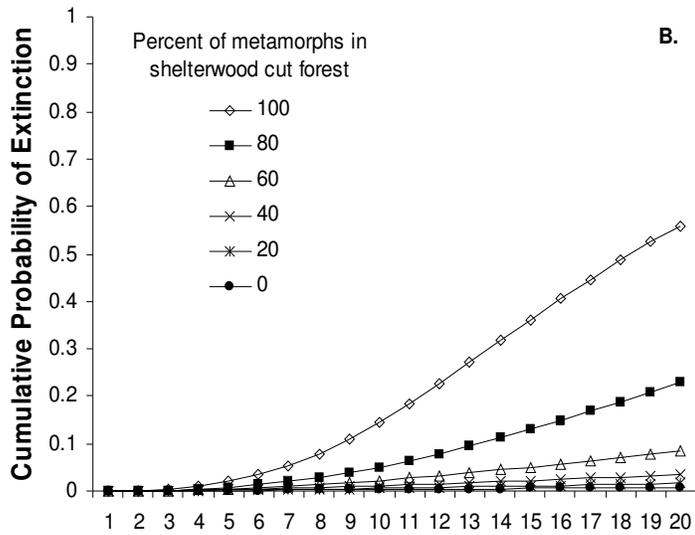
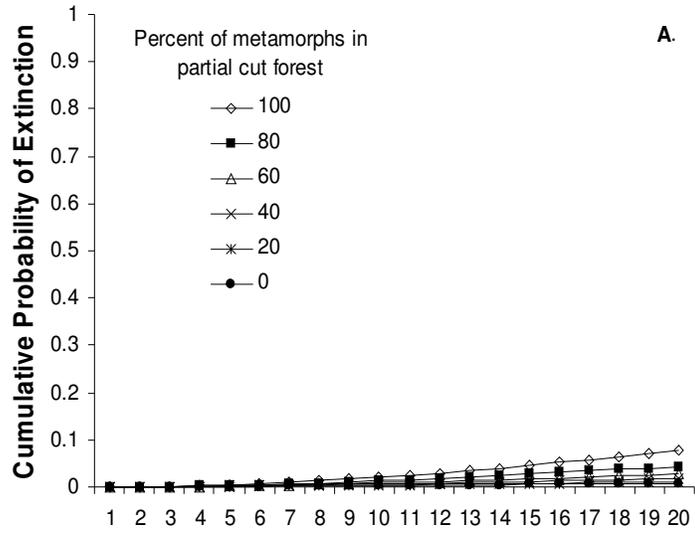
\*\* Because this is a post-breeding model, individuals must survive another year and breed the following spring

\*\*\*Survival of one-year-olds and mature adults is equal in model simulations

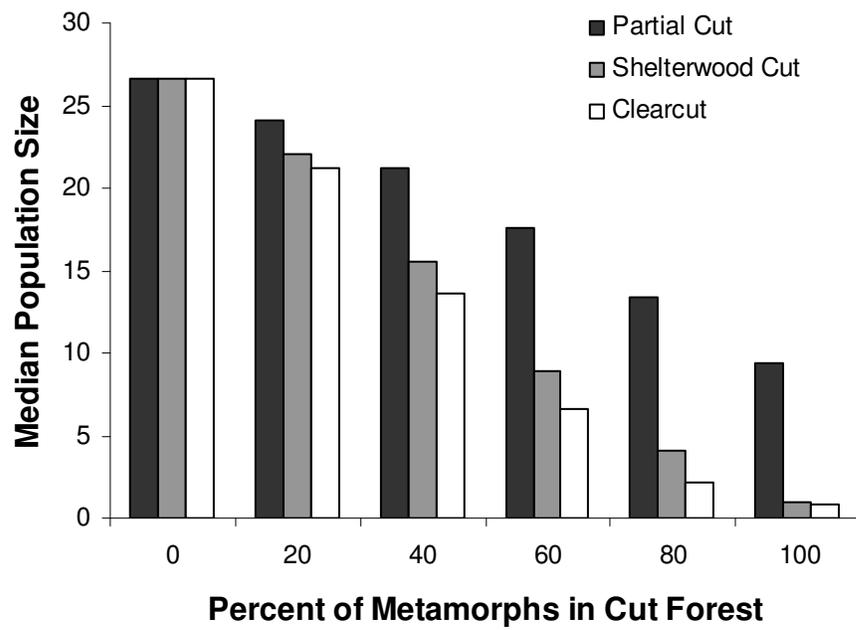
**Figure 1.** Wood frog life cycle diagram with stage specific rates of survival ( $s$ ) and fecundity ( $f$ ). The transition from egg stage to 1-year-old is a function of 3 survival rates: 1) survival of egg to metamorphosis ( $s_1$ ); 2) metamorph survival to 6 weeks ( $s_2$ ); and 3) juvenile survival from 6-weeks to 1 year ( $s_3$ ). Fecundity of one-year-olds ( $f_1$ ) is the product of clutch size, 0.50 (assuming half of the eggs are female), one-year-old survival (because the model is post-breeding and individuals must survive to the end of the year to breed), and the probability of reaching maturity and breeding before the end of the second year. Adult fecundity ( $f_2$ ) is the product of clutch size, 0.50, and adult survival. All mature adults are assumed to breed every year.



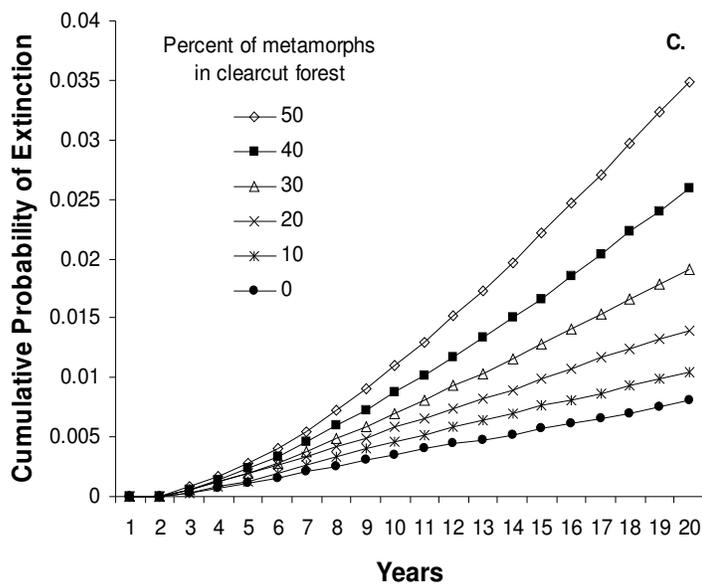
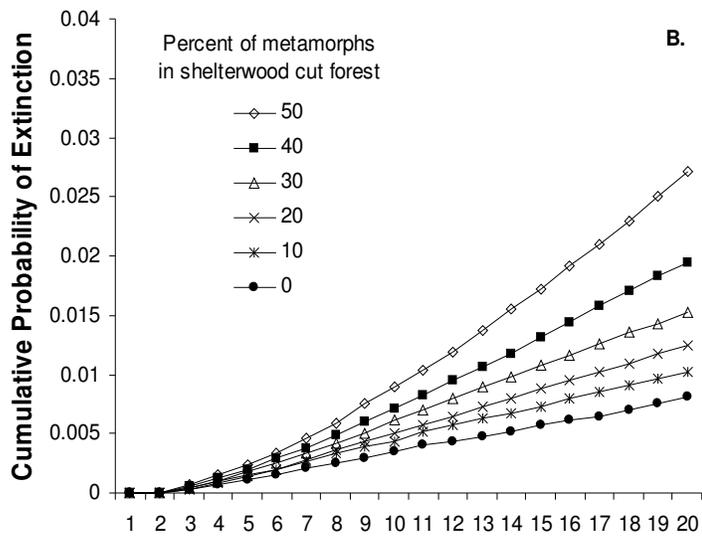
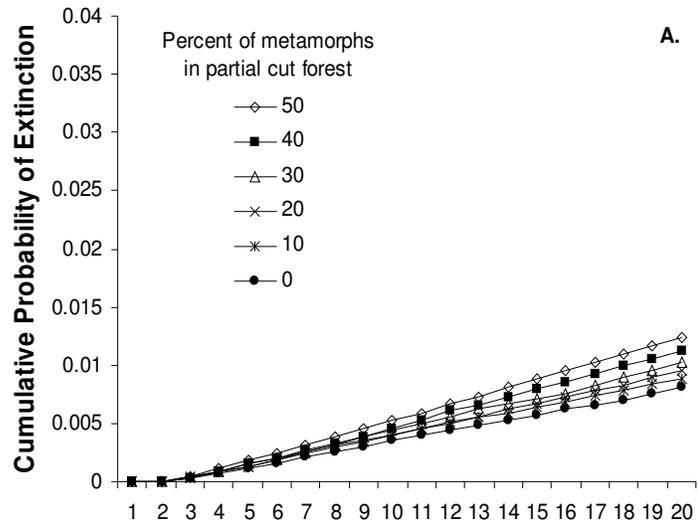
**Figure 2.** Cumulative probability of extinction over 20 years for wood frog populations in which metamorphs are exposed to one of three forestry practices: partial cuts (A.), shelterwood cuts (B.), and clearcuts (C.). Extinction probabilities increase as the proportion of metamorphs affected increases from 0 to 100%. Model predictions assume that metamorphs not affected by cuts migrate to drainage habitat (50%) and uncut forest habitat (50%).



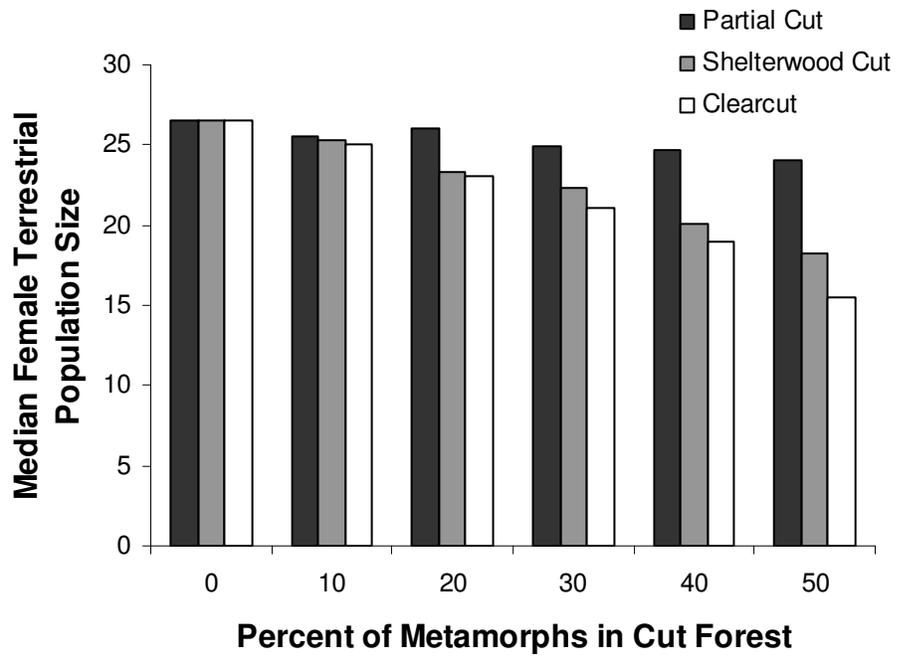
**Figure 3.** Median wood frog population size after 20 years for simulations in which metamorphs are exposed to one of three forestry practices: partial cuts (A.), shelterwood cuts (B.), and clearcuts (C.). Median population size decreases as the percent of metamorphs in the population affected by the cut increases. Model predictions assume that 50% of metamorphs not affected by cuts migrate to drainage habitat and the remaining 50% migrate to uncut forest habitat.



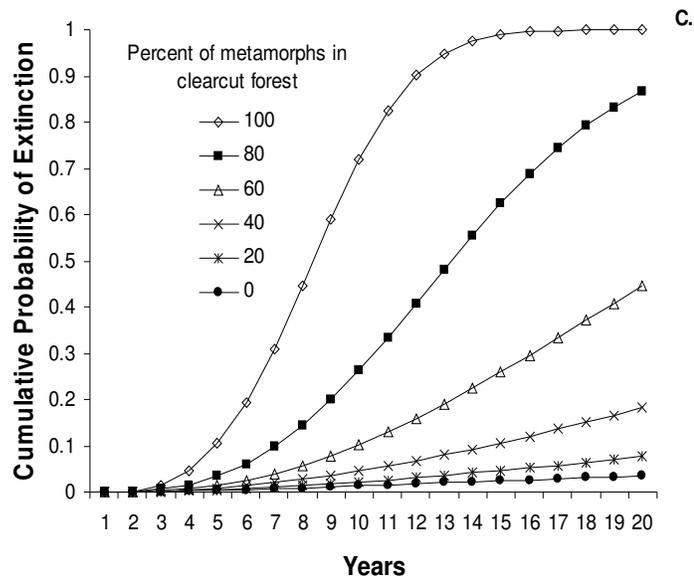
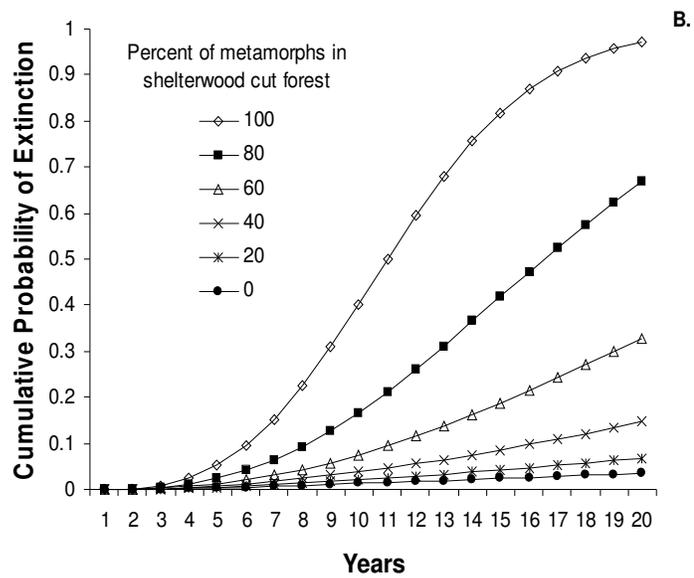
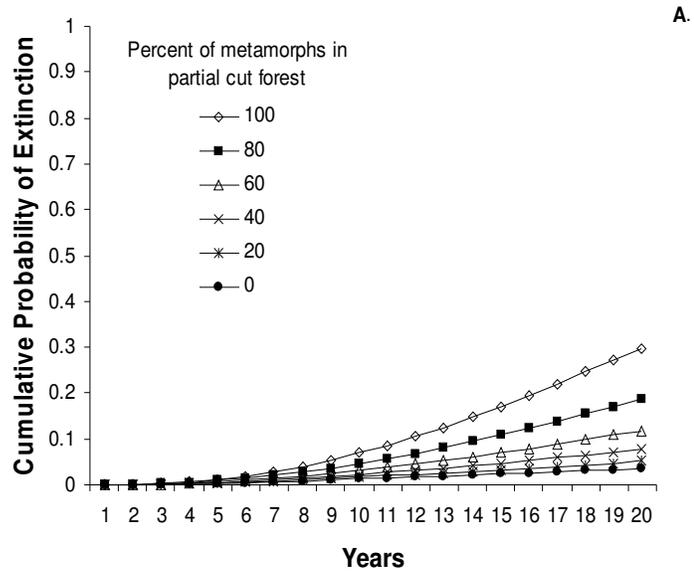
**Figure 4.** Cumulative probability of extinction over 20 years for wood frog populations in which up to 50% of metamorphs are exposed to one of three forestry practices: partial cuts (A.), shelterwood cuts (B.), and clearcuts (C.). Model predictions assume that a constant 50% of metamorphs migrate to drainage habitat and that metamorphs unaffected by cuts migrate to uncut forest habitat.



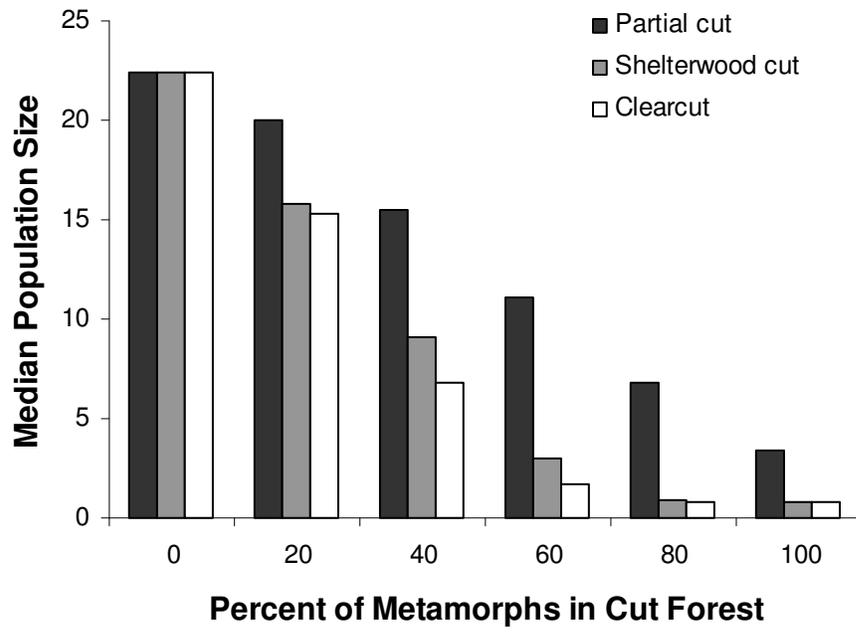
**Figure 5.** Median wood frog population size after 20 years for simulations in which up to 50% metamorphs are exposed to one of three forestry practices: partial cuts (A.), shelterwood cuts (B.), and clearcuts (C.). Median population size decreases as the percent of metamorphs in the population affected by the cut increases. Model predictions assume that a constant 50% of metamorphs migrate to drainage habitat and that metamorphs unaffected by cuts migrate to uncut forest habitat.



**Figure 6.** Cumulative probability of extinction over 20 years for wood frog populations without immigration and in which metamorphs are exposed to one of three forestry practices: partial cuts (A.), shelterwood cuts (B.), and clearcuts (C.). Model predictions assume that metamorphs not affected by cuts migrate to drainage habitat (50%) and uncut forest habitat (50%).



**Figure 7.** Median wood frog population size after 20 years for simulations without immigration and in which metamorphs are exposed to one of three forestry practices: partial cuts (A.), shelterwood cuts (B.), and clearcuts (C.). Median population size decreases as the percent of metamorphs in the population affected by the cut increases. Model predictions assume that metamorphs not affected by cuts migrate to drainage habitat (50%) and uncut forest habitat (50%).



## CHAPTER 6

### CONCLUSIONS, CONSERVATION IMPLICATIONS AND FUTURE DIRECTIONS

The maintenance of viable pond-breeding amphibian populations requires a sufficient quantity and quality of terrestrial habitat as well as connectivity among local populations. Land-use practices that affect any of these aspects of terrestrial habitat can reduce the size and viability of local amphibian populations. Evaluation of the effects of specific land-use practices can be greatly enhanced through an understanding of amphibian population dynamics and use of demographic models. Models can quantify the risks associated with a range of land-uses and provide a basis for the implementation of well informed conservation policy.

### CONCLUSIONS AND CONSERVATION IMPLICATIONS

#### *Population viability*

1. Changes in terrestrial habitat that reduce survival rates of the terrestrial life history stages of pond-breeding amphibians can lead to population declines and extinctions even if aquatic breeding habitat is protected (Chapters 2 and 4).
2. Current policies that require the maintenance of terrestrial buffers of 30 m or less around wetlands do not protect sufficient core terrestrial habitat to maintain viable populations of pond-breeding amphibians (Chapter 2).

3. A high probability of population persistence for pond-breeding amphibians requires not only a minimum area of core terrestrial habitat, but also the maintenance of habitat quality within the core habitat area. The area within 165 m of aquatic breeding sites should be considered 'core habitat' and an additional 'buffer zone' around this area should be in place to ensure that the core habitat quality remains high (Chapter 2). This is especially important for longer-lived species whose population dynamics depend on high adult survival rates to maintain stability.
4. Land-use practices that reduce or prevent immigration can severely reduce population viability (Chapters 2 and 5). Maintenance of connectivity among local populations is essential for the long-term viability of amphibian populations. Conservation measures aimed at increasing immigration rates should protect high quality terrestrial habitat between existing ponds. Immigration could also be improved by increasing in the number of breeding sites with intermediate hydroperiods in the landscape, thereby decreasing the distance between breeding sites and maximizing the number of metamorphs produced.
5. In some circumstances, the probability of persistence of a local population may remain high while the size of the local population is substantially reduced. To evaluate the success of a specific policy or land management plan it is necessary to specify whether the goal is to prevent the extinction of local populations or to maintain ecological function (Chapter 2).
6. Model simulations demonstrated that changes in juvenile survival resulting from forestry practices can have substantial population level effects, increasing

extinction probabilities up to 100%. However, the magnitude of these effects depended greatly on both the type of forestry practice employed as well as the proportion of emerging metamorphs affected (Chapter 5). While some forestry practices could lead to the extinction of local populations, it is possible to carry out small scale cuts while still maintaining wood frog population viability, provided sufficient areas of suitable habitat are protected.

### ***Population dynamics***

1. Density in the terrestrial stage can reduce growth, survival and reproductive development. Terrestrial density dependence may play an important role in amphibian population regulation and should be considered in models of amphibian population dynamics (Chapter 3). As areas of suitable terrestrial habitat are reduced and degraded, carrying capacities in the terrestrial environment will likely be reduced, and the effects of terrestrial density may play an even greater role in the dynamics and decline of amphibian populations.
2. A large proportion of the mortality experienced by juvenile amphibians in their first year occurs within the first 6 weeks following metamorphosis (Chapters 3 and 4). Stage-structured demographic models that consider this time period to represent a separate stage can offer more accurate evaluations of potential conservation strategies.

### ***Forestry effects on amphibian survival***

1. We found that forestry practices interact with existing landscape structure to determine microclimate and thereby influence amphibian survival. Land managers should consider that a particular forestry practice may have very

different consequences for amphibians depending on the topography of a site (Chapters 4 and 5).

2. Maximum ground surface temperature was the best single predictor of wood frog and American toad survival across a range of forestry practices. This variable functions as an accurate composite measure of the effects of both forestry practices and landscape structure, because it is determined by multiple factors (Chapter 4).

### *Species comparisons*

1. Species with different life history strategies responded differently to terrestrial habitat loss and degradation in our simulations. Species with a short lifespan and high fecundity (wood frogs) were most sensitive to habitat loss and isolation, while longer lived species with lower fecundity (spotted salamanders) were most sensitive to long-term habitat degradation (Chapter 2).
2. Survival was greater for metamorph wood frogs than for American toads in both terrestrial enclosure experiments (Chapters 3 and 4). Although American toads are considered to be habitat generalists whereas wood frogs are forest dependent, toad metamorphs are highly susceptible to desiccation due to their small size and are sensitive to changes in habitat quality.

### *Conservation of wood frogs at the edge of their range*

1. Wood frog populations are highly prone to stochastic extinction and are dependent on re-colonization for long term persistence. Conservation of this species requires that connectivity among local populations be maintained. Isolating wood frog populations from the possibility of re-colonization results in

high probabilities of local extinction even when sufficient terrestrial habitat is maintained to support the local population (Chapters 2 and 5).

2. The extremely variable rates of survival that we observed for juvenile wood frogs suggest that on the edge of their range, wood frogs are only able to survive in a small subset of the microhabitats that occur within the landscape. Conservation strategies aimed at protecting wood frog populations on the edge of their range should identify areas of suitable terrestrial habitat where conditions are cool and moist such as drainages and north-facing slopes, and ensure that land-use practices do not degrade these areas or cut off access to them (Chapter 4).

## **FUTURE DIRECTIONS**

As more data become available, amphibian demographic models can increase in accuracy and in the range of conservation questions they are capable of answering. I will be working as a post-doc with James Gibbs at SUNY-ESF in a continuation of the LEAP project to develop spatially explicit metapopulation models that incorporate aspects of amphibian movement behavior. These models will be based on data gathered at all three LEAP sites: Maine, Missouri and South Carolina, and will allow species-specific and region-specific comparisons to be made.

## APPENDIX

### COMPARISON OF WOOD FROG DEMOGRAPHIC MODELS FOR NORTH-EASTERN POPULATIONS (CHAPTER 2) AND MISSOURI POPULATIONS (CHAPTER 5)

The wood frog demographic models developed in chapters 2 and 5 differ in their structure and parameterization primarily because they are intended to represent populations from two very different geographic regions. Several studies of wood frogs have shown that demographic parameters including time to reproductive maturity, clutch size and annual survival rates exhibit substantial geographic variability (Berven 1988; Berven 1995; Sagor et al. 1998). The model in chapter 2 represents populations typical of the northeastern U.S. while the model developed in chapter 5 focuses on wood frog populations in the Midwest, specifically in Missouri. In chapter 2, the goal of the modeling process was to estimate the population-level responses of wood frogs to loss and degradation of terrestrial habitat resulting from human land-use. To make these conclusions relevant across as broad a range as possible we used demographic data from populations in the contiguous north-eastern portion of the wood frogs' range. This is the region where the most detailed demographic data are currently available for wood frogs and is also a region where many land-use policies at the state and local levels are currently being revised and could benefit from additional conservation recommendations. The model developed in chapter 5 was designed to address questions unique to threatened wood frog populations at the edge of their range in Missouri where population sizes and

demographic rates differ from those of northeastern populations. However, very few demographic data are available for wood frogs in this region (Muths et al. 2005), therefore in developing the model it was necessary to use a combination of data from Missouri, from similar sites nearby in Illinois, and in some cases from populations in the northeast. Data sets from wood frog populations in Missouri, collected as part of the Land-use Effects on Amphibian Populations (LEAP) project, allowed us to incorporate density dependence (results presented in Chapter 3) and forestry effects (results presented in Chapter 4) in the Midwestern model, whereas these effects were not included in a functional form in the northeastern model. Below are comparisons of the model structure and initial population vectors for the demographic models developed in chapters 2 and 5. Parameter estimates used in the two models are summarized for comparison in Table 1.

## **MODEL STRUCTURE**

The two wood frog demographic models differ slightly in structure due to the data available for each region. For the northeastern model we used life table data from a 7-year study of wood frogs in a Maryland pond that followed 5 cohorts of metamorphs through reproductive maturity (Berven 1990). Data in this format provide age-specific rates of survival and fecundity which lend themselves well to an age-based rather than stage-based model. However, because the life history stages that comprise the first year of a wood frog's life (egg, larvae, and juvenile) experience very different survival rates, we developed a hybrid age/stage based model with the following classes: 1) Pre-metamorph (egg and larval stages); 2) One-year-old; 3) Two-year-old and 4) Three-year-old. Life table data are not available for wood frog populations in the Midwest and

therefore we were unable to determine age-specific rates of survival, rather we developed a stage-specific model comprised of the following stages: 1) egg to one-year; 2) one-year-old; 3) mature adult. Both models are post-breeding, female-only models.

### **INITIAL POPULATION SIZE**

Wood frog population sizes tend to be much larger in the northeast than in the disjunct populations found in Missouri. For both models we based initial population vectors and maximum carrying capacity (modeled as a cap on population size) on egg mass surveys conducted in each region. Data for the northeastern region came from Egan and Paton's (2004) surveys of 124 randomly selected ponds in Rhode Island. Wood frogs occurred in 69% of the ponds, and most occupied ponds contained more than 50 egg masses (mean: 184, range 1 – 1,033). The cap on population size in the northeast model was set at 1,033 breeding females (one and two-year-olds) and the 10 initial population vectors included a range of 5 to 1033 breeding females. For the Midwestern model we used egg mass survey data from 33 breeding sites in Daniel Boone Conservation Area in Missouri (Tracy Rittenhouse unpublished data). In these surveys, nearly all occupied sites contained fewer than 30 egg masses, and the maximum number of egg masses at a single site was 97. In the Midwestern model we set the cap on population size at 97 and used a range of initial population vectors that included 3 to 21 one-year-old females and 4 to 26 adult females.

**Table 1.** Comparison of range and means of demographic variables used in models of wood frog populations in the northeast (Chapter 2) and Missouri (Chapter 5).

<b>Parameter</b>	<b>Northeastern Model</b>		<b>Missouri Model</b>	
	<b>Range</b>	<b>Mean</b>	<b>Range</b>	<b>Mean</b>
Egg survival to metamorphosis	0 – 0.095	0.046	0 – 0.060	0.019
Metamorph survival to one year	0.25 – 0.50	0.38	0.096 – 0.62	0.38
1-year old survival to 2-year old	0.14 – 0.61	0.29	0.34 – 0.52	0.41
2-year-old survival to 3-year old	0.08 – 0.23	0.13	0.34 – 0.52	0.41
Pre-metamorph fecundity	0 – 0.26	0.095	0	0
1-year-old fecundity	41 – 229	98	24 - 56	41
2-year-old fecundity	29 – 69	43	109 - 257	187

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## VITA

Elizabeth Burnham Harper was born on 11 September 1978 in Kansas City, Missouri. She graduated from Shawnee Mission East High School in Kansas and earned a B.A. in Biology from Middlebury College in Vermont. While at Middlebury she worked as a field assistant for Dr. Janie Wulff on research in mangrove and coral reef communities in Panama and for Dr. Helen Young assisting with studies of nectar robbing bees in Vermont. She began research on leaf litter frogs in Costa Rica during a course through the Council on International Education Exchange, and returned to Costa Rica the following year to complete a senior thesis project under the guidance of Stephen Trombulak. After graduating from Middlebury, Elizabeth received a Watson Fellowship, allowing her to study amphibians in Thailand, Australia, Tanzania and Venezuela. Elizabeth began graduate studies at the University of Missouri in 2003 under the guidance of Raymond Semlitsch. In 2005 she married David Patrick, whom she had met while working in Tanzania. She earned her Ph.D. from the Division of Biological Sciences in May 2007. She and her husband will both be conducting post-doctoral research under Dr. James Gibbs at the State University of New York College of Environmental Science and Forestry in Syracuse New York. In the future, Elizabeth plans to continue conducting research in the field of amphibian conservation.